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JOURNAL OF THE ROYAL SOCIETY OF ARTS

No. 4710 *FRIDAY, FEBRUARY 1st*, 1946 Vol. XCIV

CHAIRMAN OF COUNCIL

At the meeting of the Council held on Monday, January 21st, Viscount Bennett was unanimously elected Chairman of the Council.

MEMORIAL SERVICE FOR DR. E. F. ARMSTRONG, F.R.S.

A Memorial Service for Dr. E. F. Armstrong, F.R.S., Chairman of the Council, was held at St. Martin-in-the-Fields, at 2.30 p.m. on Thursday, January 17th.

The service was conducted by the Rev. Eric Loveday, Vicar, and the address was given by the Rev. A. G. B. West, Rector of St. Dunstan-in-the-East.

In addition to Mrs. Armstrong, Captain R. G. Armstrong and Miss Joyce Armstrong and other relatives, the large congregation included the Rt. Hon. J. Chuter Ede, the Home Secretary; representatives of the Ministry of Works; the British Association; the British Association of Chemists; the British Iron and Steel Federation; the British Standards Institution; the Imperial College of Science; the Oil and Colour Chemists' Association; the Royal Institution; the Royal Society; the City and Guilds of London Institute; the Commercial Gas Company; the South Metropolitan Gas Company; the South Suburban Gas Company and other bodies with which Dr. Armstrong had been connected.

Mr. Winston Churchill was represented by Mrs. R. E. K. Hill.

Viscount Bennett, President of the Society, was represented by Mr. J. A. Milne, C.B.E. Other members of the Council present were Sir Frank Brown, Sir Atul Chatterjee, Sir Edward Crowe, Sir Edward Gait, Miss Caroline Haslett, Mr. Oswald Milne, Mr. J. W. Ramsbottom, Mr. E. M. Rich, Mr. E. M. Runtz, Captain A. H. Ryley (representing the Deputy Master and Elder Brethren of Trinity House), Mr. William Will and Mr. J. G. Wilson.

The following members of the Council expressed regret at being unable to be present:—Professor E. C. Dodds, Sir Thomas Dunlop, Mr. E. W. Goodale, Sir Henry McMahon and Mr. Rex Roberts.

The following Fellows of the Society attended*:—

Mr. R. M. Astbury, Mr. John Bacon (representing the Circle of Glass Collectors), Mr. H. J. Brown, Mr. Francis F. Cass, Mr. J. T. Davis, Mr. Henry Dowling, Dr. Vargas Eyre, Mr. W. G. Freeman, Miss A. Gordon French, Professor C. S. Gibson, Mr. Percy Good, Squadron Leader C. S. Goode, Mr. C. J. Goodwin, Mr. A. Kirkham Hamilton, Mr. Leslie Hardern (Public Relations Officer, the Gas Light & Coke Company), Mr. L. A. Thoywell Henry, Dr. T. A. Henry (representing the Wellcome Foundation Limited), Lt.-Comm. F. A. de Vine Hunt, Mr. H. W. Johnson, Mr. James Kewley, Dr. H. Kraus, Dr. L. H. Lampitt, Lord Leverhulme, Dr. D. C. Martin (Secretary of the Chemical

* This list was compiled from the list of names collected by the Representative of *The Times* whose assistance is acknowledged with thanks.

Society), Mr. D. R. G. Mason, Miss Helen Masters, Mr. C. F. Merriam, Mr. A. J. Munro, Mrs. Patrick Ness (representing the National Council of Women), Mr. T. C. Norris, Dr. W. G. Ogg (Director, representing Rothamsted Experimental Station), Dr. C. C. Paterson (representing the British Standard Institution), Mr. J. E. Roberts, Mr. H. S. Shield, Mr. André L. Simon, Professor J. L. Simonsen (representing the Chemical Society), Mr. Percy Delf Smith, Engineer Rear Admiral A. Turner, Mrs. H. M. Whitlow and Mr. W. S. Lloyd Willey.

Lord Broughshane and Mr. Alfred C. Bossom were represented.

Messages of regret from, or on behalf of, the following Fellows were received :— The Rev. C. B. Bartlett, Mr. Howard Coster, Mr. Vernon W. Davies, Sir Robert Graham, Major J. G. Jeffrey, Mr. Francis Meynell, Mr. Leonard E. Strong and Mr. P. W. Thompson.

Admiral of the Fleet, Lord Chatfield (President) and Major-General Sir Fabian Ware represented the War Memorials Advisory Council. The Clerical Officer, Mrs. E. D. Hardwick, was also present.

The following officials and members of the Staff of the Society attended the service :— Miss J. Scott Rogers (Acting Secretary), Mrs. I. Dummett (Acting Assistant Secretary), Mr. A. G. Toye (Accountant), Mr. H. T. Broad (Examinations Officer), Mr. G. A. Nicholls (Head of the Printing Department) and Mr. W. T. Tuck (Acting Chief Clerk).

HOUR OF SOCIETY'S MEETINGS

The Council have agreed to continue the practice of holding meetings at 1.45 p.m. and in certain cases at 5.15 or 5.30 p.m., for the remainder of the present session, after which the matter will be reviewed in the light of existing transport facilities and other considerations. Times will, in all cases, be clearly announced in the *Journal*.

PUBLICATION OF LIST OF FELLOWS

For the first time since 1938, an up-to-date List of Fellows of the Society, corrected to November 8th, 1945 inclusive, is now available. Miss Anna Zinkeisen, R.D.I., has designed a special cover. It is hoped from henceforth to continue the pre-war practice of publishing the list annually.

Although stocks of the present issue are necessarily limited, the Acting Secretary will be pleased to send a copy, free of charge, to any member who applies for one.

MEETINGS OF THE SOCIETY TO THE END OF FEBRUARY

Ordinary Meetings

Wednesdays, at 1.45 p.m. (unless otherwise stated).

February 6.—(At 5.30 p.m.) (*Trueman Wood Lecture.*) "Nuclear Energy and its Peace-time Applications." By Professor C. D. Ellis, F.R.S., Scientific Adviser to the Army Council. The Right Hon. Sir John Anderson, G.C.B., G.C.S.I., G.C.I.E., F.R.S., will preside.

February 13.—(At 5.30 p.m.) (*Fothergill Lecture.*) "A Scientific Approach to Fire Fighting and Prevention." By Professor G. I. Finch, M.B.E., D.SC., F.R.S., formerly Scientific Adviser to the Ministry of Home Security. The Right Hon. Viscount Falmouth, Head of the Fire Research Division, Home Office, will preside.

February 20.—"Radar and the Magnetron." By J. T. Randall, D.SC., Professor of Physics, University of St. Andrews. (Illustrated by lantern slides and demonstrations.)

N.B.—*As accommodation is limited, seats can only be reserved for Fellows and their friends if application is made in advance to the Acting Secretary.*

February 27.—"The Appreciation of Greek Art." By Charles Seltman, Director of the Greek Exhibition, 1946, Royal Academy. (The lecture will be illustrated by epidiascope.)

India and Burma Section

Thursday, at 2.30 p.m.

February 7.—(*Sir George Birdwood Memorial Lecture.*) "The Health of India." By Major-General Sir John Megaw, K.C.I.E., I.M.S.(ret.), President, India Office Medical Board and Medical Adviser to the Secretary of State for India, 1933–1939. Sir John A. Woodhead, K.C.S.I., C.I.E., Adviser to the Secretary of State for India, will preside.

Dominions and Colonies Section

Tuesday, at 1.45 p.m.

February 19.—"The Work of Kew in the Interests of the Overseas Empire." By Professor E. J. Salisbury, C.B.E., D.SC., F.R.S., Director of the Royal Botanic Gardens, Kew. The Right Hon. Viscount Bennett, P.C., K.C., LL.D., President of the Society, will preside.

Cantor Lectures

Mondays, at 1.45 p.m.

February 4.—(Third of a series of three Lectures.) "High Speed Flight." By Dr. S. G. Hooker, B.SC., D.I.C., Assistant Chief Engineer, Rolls-Royce, Ltd. (Illustrated by lantern slides.)

Lecture III.—Flight in the Future? Aircraft performance in the stratosphere. High altitude civil machines with gas turbine engines. The problem of the pressure cabin and air conditioning at high altitude and speed. The passage through the sonic barrier. Rocket propulsion. The future of athodyds and supersonic flight. Atomic energy and the aeroplane.

February 18, 25 and March 4.—(Three Lectures.) "Modern Textile Fibres (Cellulose acetate, cuprammonium, viscose, nylon, protein, vinyon, glass, etc.)."

Lecture I.—The Manufacture of Modern Textile Fibres. By Claude Diamond, B.SC., F.R.I.C. Expansion of the industry. Principles of manufacture. Classification of fibre polymers. Raw materials. Fibre structure. Function of viscosity. Fibres from natural organic polymers —regenerated celluloses, cellulose acetate, proteins, alginate. Fibres from laboratory made polymers—polyamides, vinyls. Glass fibre.

Lecture II.—The Chemical and Physical Properties of Modern Textile Fibres. By John K. Berry, M.SC., A.INST.P. Differences in chemical nature. Thermal properties. Mechanical properties and the range available. Stress strain and the effect of conditions of measurement. Structure in relation to mechanical properties. Moisture absorption and imbibition. Elasticity. Resistance to chemical attack. Dyeing properties.

Lecture III.—The Application of Modern Textile Fibres. By Robert S. Greenwood, M.SC.(TECH.). Brief historical survey. Economic, political and social facts and influences. Textile uses of the various rayons, nylon and plastic fibres for wearing apparel, furnishing and domestic, engineering, industrial and war purposes.

N.B.—*In cases where meetings begin at 1.45 p.m., a sandwich luncheon, at 1s. 9d. per head, will be available if ordered from the Housekeeper the day before the meeting.*

MEETING OF COUNCIL

A meeting of the Council was held on Monday, January 21st, 1946.

Present: Viscount Bennett (in the Chair); Lord Aberconway; Mr. F. H. Andrews; Mr. Henry Berry; Sir Frank Brown; Major W. H. Cadman; Sir Thomas Dunlop; Sir Edward Gait; Mr. E. W. Goodale; Mr. Basil Ionides; Sir Henry McMahon; Mr. G. K. Menzies; Mr. J. A. Milne; Mr. O. P. Milne; Mr. Keith Murray; Sir Ernest Pooley; Mr. J. W. Ramsbottom; Mr. E. M. Rich; Mr. A. R. N. Roberts; Captain A. H. Ryley; Mr. William Will; Mr. J. G. Wilson and Miss Anna Zinkeisen, with Miss J. Scott Rogers (Acting Secretary).

It was unanimously agreed that Viscount Bennett be appointed Chairman of the Council.

It was unanimously agreed that Viscount Samuel be elected a Vice-President to fill the vacancy created by the death of Dr. Armstrong.

The following were duly elected Fellows of the Society:—

Bousfield, Colonel Hugh Delabere, C.M.G., D.S.O., D.L., T.D., B.A., LL.D., Leeds.
Brady, Thomas Cullen, Edinburgh.
Brown, Raymond Gordon, London.
Buchanan, Robert, Glasgow.
Card, Captain Raymond William George, Toronto, Canada.
Carter, Leonard James, London.
Corser, Haden, Worcester Park, Surrey.
Cruikshank, Robert James, London.
Goodchild, Raymond Bertram, Hatch End, Middlesex.
Gray, Leslie Jack, Bournemouth, Hants.
Hurst, Albert Edward, Darwen, Lancs.
Latham, The Right Honourable Lord, J.P., London.
Mansbridge, John, London.
Markham, Miss Violet Rosa, C.H., D.LITT., LL.D., London.
Nethersole, Harrison John Hastings, B.SC., Ashby de la Zouch, Leics.

Newman, Leonard Alfred William, Thornton Heath, Surrey.
Owen, George Reuben Bertram, Eccles, Manchester.
Peet, Alexander, Luton, Beds.
Stirrup, John, Blackburn, Lancs.
Timms, Thomas Samuel, Exeter, Devon.
Tripp, Edward Howard, PH.D., London.
Willis, Mrs. Alice Liddle Hedley, Walsall, Staffs.
Wreford, Herbert Denis, London.
Young, Lieut.-Colonel Thomas, London.

The following was duly elected an Associate of the Society :—

Lee, John Derek, Keighley, Yorks.

The death of two of the Society's examiners was reported with regret. (See Obituary Notices on pp. 168-9 of this issue).

It was reported that the Metropolitan Drinking Fountain and Cattle Trough Association had agreed to the terms suggested by the Society for the organisation of a competition for improved designs in drinking fountains.

A gift to the Society from Lord Catto, Governor of the Bank of England, of a printed copy of a drawing of London made by an A.R.P. Observer from the roof of the Bank in the summer of 1944, was reported.

A quantity of formal and financial business was transacted.

PROCEEDINGS OF THE SOCIETY

CANTOR LECTURES

VIRUS DISEASES OF PLANTS

By F. C. BAWDEN, M.A., *Head of the Department of Plant Pathology, Rothamsted Experimental Station*

[*Note.*—This course consisted of three lectures which were delivered on November 19th and 26th and December 3rd, 1945. In preparing them for the press the lecturer has decided to run the lectures together in order to present a more consecutive story.]

INTRODUCTION

The literal meaning of the word "virus" is a poison or toxin. This is unfortunate, because the diseases we shall be discussing are not simple effects of poisoning ; they are among the most infectious of diseases and their causes, the viruses, multiply with great readiness in the infected plants. To reduce confusion as much as possible, therefore, I will start by trying to define what we mean when we speak of a virus disease. This is probably best done by a short historical digression.

In the latter half of the eighteenth century after the germ theory of disease was established, it was confidently believed that for each disease would be isolated a specific bacterium or fungus which could be grown on culture medium and identified by the usual microscopic and cultural techniques. This belief met with a rude shock when in 1892 it was shown that bacteriologically sterile filtrates of juice from tobacco plants suffering from mosaic were infective, and caused mosaic when injected into healthy plants. So viruses were discovered ; and for a time they could be precisely defined as infective agents capable of passing through bacteria-proof filters. But this did not last long, and few of the 200 or so plant virus diseases now identified have been shown to be caused by filter-passers. There are good reasons for this, such as the difficulty of getting infections with extracts of plants infected with many different viruses and the unsuitability of plant extracts as a filtering medium, but these need not be discussed here. Suffice it to say, that filterability as a criterion of a virus has been largely replaced by invisibility, and the only features that all the recognised virus diseases are known to share are, first, that they are infectious and, secondly, that no causative pathogen can be identified with microscopes using visible light. Thus, when we speak of a virus disease, we mean merely an infectious disease with an invisible cause. Another feature that viruses have in common is that none has yet been induced to multiply except in living cells. The significance of this is difficult to assess, because serious attempts at cultivation have been made with only a few viruses, but it seems likely for other reasons that viruses are in fact obligate parasites.

With two such negative features as invisibility and inability to multiply *in vitro* providing the bases for grouping, it would not be surprising if our viruses covered a range of different kinds of entities. This may be so, for we find great differences between individual viruses in the type of symptom they cause, in the way they are transmitted, in the range of plants they can infect and in their resistance to physical and chemical treatments. However, as we shall see later, the plant viruses that have so far been studied in any detail have all been found to be the same type of agent,

each having been isolated in the form of a nucleoprotein. These viruses differ from one another in many of their properties, and it is almost certain that other viruses will also be found to be nucleoproteins. But less than 5 per cent. of the known plant viruses have yet been purified, and it would be rash to assume that they are a random selection representative of the whole group. Only further work on a wider range of virus diseases can show whether the present chemical uniformity of viruses is real or if it is only a temporary phase in our knowledge arising because of fortuitous methods of selecting viruses for study.

External Symptoms

As viruses are invisible their existence cannot be recognised directly, but only by observing the visible effects they produce. Few or no generalised statements can be made about these effects to which there are no exceptions, but there are a number that are common to many virus diseases. Some plants, the carrier types, can be infected with a virus without showing any effects at all, and for the detection of a virus in these we are dependent on the production of symptoms when transmissions are made to other varieties or species. As the infected carrier cannot be distinguished by eye from uninfected plants, the roguing of carriers is impossible so that stocks usually soon become 100 per cent. infected and provide dangerous, and often unsuspected, sources of infection for intolerant plants.

The most important as well as the most common effect of virus infection is a reduction in the cropping power. This is usually accompanied by other obvious changes, of which the most frequent are a dwarfing or stunting of the plant (Fig. 1), and an alteration in the colour and shape of the leaves. Instead of being uniformly green, the leaves develop spots, patches, rings or other patterns, of light green, yellow, white, brown or black, or the whole leaf may look generally chlorotic without obvious mottling. These conditions are responsible for the common names, such as mosaic, ringspot, streak and yellows, which are usually given to virus diseases. Deformity of the leaf may also show as an alteration in the leaf outline, as a crinkling or puckering, or the laminæ may be so reduced that the leaves consist of little more than the main veins and resemble tendrils ; these conditions give rise to such names as crinkle, fern-leaf and bootlace (Fig. 2). Although the most common effect is to reduce size and vigour, local stimulation of growth occurs in several diseases. This may take the form of unusual outgrowths from the leaf (enations) or gall-like proliferations in stems and roots. Symptoms may also occur on flowers and fruit. A mosaic of self-coloured flowers such as tulips and wallflowers is one of the more striking effects of virus diseases (Fig. 3). The " broken " tulip was for long prized as a more beautiful specimen than its uniformly coloured ancestor, and many varied recipes were advocated by growers to produce the desired effect. Now that broken tulips can be produced at will and are known to be the result of virus infection, they are no longer wanted, and the mottled flower is regarded as an intruder spoiling the uniformity of a planned colour scheme. On fruits such as the tomato and cucumber a mosaic suggesting uneven ripening is a frequent symptom, and evidence is accumulating that more serious troubles such as " chat " fruit of apples and stony pit of pears are also effects of virus diseases.

The symptoms of most commonly occurring virus diseases are not usually difficult to distinguish from those of other kinds of infectious diseases, for they tend to occur more uniformly over the whole plant than with bacterial or fungal infections. This is because in most natural infections the virus spreads from its original entry point throughout the vegetative parts of the plant. Virus diseases are more likely to be confused with the effects of unfavourable soil conditions such as deficiencies of essential mineral elements or the presence of toxic substances, such as copper or sodium chlorate, than with foliage diseases caused by other pathogens. Damage to the base of a plant, however, may simulate the appearance of a systemic infection : the symptoms characteristic of potato leaf roll, for example, are sometimes produced by fungi attacking the base of the plant or by mechanical injury to the stem.

Unless a range of differential hosts is used, symptoms are unsatisfactory as a basis for identifying specific viruses. The same virus may cause widely different symptoms in different species, or even different varieties of the same species, and in the same plant symptoms may vary with the age and nutrition of the host, and with the environmental conditions. A virus that causes a necrotic, lethal disease in one potato variety, may produce a mild mosaic in a second, and be carried without symptoms by a third : and, in the variety that shows mosaic, symptoms may be

suppressed if the temperature rises to above 20° C. Another factor that complicates diagnosis from symptoms is that different viruses may cause almost identical symptoms in the same host; fern-leaf of tomato, for example, may be produced by infection with either cucumber mosaic virus or tobacco mosaic virus.

In many virus diseases there are three successive phases. As a result of multiplication of virus at the entry points, lesions first appear on the inoculated leaves. The virus moves slowly from cell to cell through the leaf tissue, but when it reaches the phloem it travels rapidly to distant parts of the plant. It does not seem to have any powers of independent movement, but seems to travel passively in the stream of elaborated food materials. Thus, its movement is away from tissues that are producing more food by photosynthesis than they need and towards regions of active growth. It is because of this, and not because they resist infection, that leaves which are fully developed at the time the plant becomes infected rarely show symptoms. If such leaves are directly inoculated, or kept in the dark so that the flow of food materials is in their direction instead of away from them, they readily become infected. In natural conditions, however, the results of systemic infection appear first on the young, actively growing leaves and the older parts of the plant may look normal while the younger parts show severe symptoms. In many of the mosaic diseases, the young leaves first show "clearing of the veins," a pallor restricted to the regions directly adjacent to the veins, before passing to their characteristic mottled appearance. This difference between the first and second phase of systemic symptoms in mosaic diseases is slight compared with that in some others, which pass from an acute to a chronic stage. Sometimes both these stages are serious diseases; in many potato varieties, for example, the first acute stage of infection with potato virus Y is a necrotic disease, leaf-drop-streak, which is succeeded by severe mosaic (Figs. 4 and 5). But the chronic stages of some other diseases can be extremely mild. A few days after tobacco plants are infected with tobacco ringspot virus, the inoculated leaves develop necrotic local lesions. Some days later systemic symptoms appear on the young leaves as necrotic rings and spots so severe that it seems as though the plant would succumb. Instead, however, new leaves are produced on which necrotic lesions either fail to develop or develop only sparsely, while still later leaves may show only a faint greyish mottling or even look quite normal (Fig. 6). When the older, necrotic leaves have fallen such plants may be almost indistinguishable from uninfected ones, though the extent of the recovery is affected by the environment, especially by temperature. Such plants do not develop necrotic lesions if again inoculated with the ringspot virus.

This sequence of recovery from an acute disease followed by a subsequent immunity superficially resembles that in many virus diseases of animals. With animals, however, the recovery results from the production of antibodies to the pathogen, and the subsequent immunity is usually of a sterile type. Plants lack the elaborate defence mechanisms of animals; there is no circulating blood stream containing phagocytes and no evidence that plants can produce effective antibodies. Once a plant becomes systemically infected with a virus, it remains infected for the rest of its life, and the apparently normal leaves formed by plants which have recovered from tobacco ringspot still contain virus. Nothing is known of the mechanism underlying the recovery, except that the virus content of infected symptomless leaves is less than that of acutely necrotic leaves. Identical results are obtained when sap from either type of leaf is used as inoculum for healthy plants, and there is no evidence that recovery entails any change in the virulence or infectivity of the virus. Acute symptoms and a high virus content are restricted to leaves that were formed before they became infected, whereas those infected while embryonic behave as carriers. This suggests that infection of newly-formed cells affects their metabolism, possibly by preventing the formation of some normal cell component, so that the multiplication of virus is lessened and the reaction responsible for the production of necroses in normally developed cells does not proceed.

Although this sequence of events, local lesions followed by systemic symptoms of two kinds, is very common, it is by no means general. In different diseases any one phase may be omitted and some viruses give different sequences in different host plants. If the reaction of the plant to infection is of the necrotic type, symptoms may be restricted to local lesions. For instance, tobacco mosaic virus, which produces a systemic mottling and no visible local lesions in *Nicotiana tabacum*, gives only necrotic local lesions when inoculated to *Nicotiana glutinosa*. This phenomenon is probably merely a reflection

of the fact that the virus is an obligate parasite. If the originally infected cells react so acutely that they die before the virus has multiplied sufficiently to move to other tissues, multiplication ceases and the virus is restricted to the local lesion. Such local lesions are extremely valuable in research work on the viruses, because the numbers produced can be used as a measure of the infectivity of a virus preparation and counts of such lesions afford a method of comparing the relative infectivities of different preparations. This type of reaction also affords a considerable opportunity to the plant breeder of reducing losses from virus diseases, because in nature viruses are rarely found to any extent in stocks of plants that are hypersensitive, whereas they are widespread in those which react by producing a systemic mosaic. The ability of *N. glutinosa* to localise infection with tobacco mosaic virus is the effect of a single dominant gene, which has now been transferred to *N. tabacum* by crossings through *N. digluta*. If this gene can be incorporated into tobacco varieties of good commercial qualities, it should do much to reduce the losses now caused by this virus. Not only will it reduce the losses in the tobacco crop itself, but it should help to protect crops such as tomato, the initial infection of which often comes from contaminated tobacco.

Similarly, there are the possibilities of reducing losses from potato mosaic viruses by breeding hypersensitive varieties. Several varieties are already widely grown that react either with local lesions only or else die with a lethal systemic necrosis when infected with one or other of potato viruses A, B, C and X. Commercial stocks of such varieties are rarely found infected with a virus to which they are hypersensitive, for such varieties in effect do their own roguing. By contrast, stocks of varieties which react to these viruses with mosaic symptoms are usually heavily infected unless drastic roguing and selection have been practised. By crossing between different varieties, Craig's Defiance has been bred, which is hypersensitive to all four viruses. The production of such intolerant plants promises to be much more valuable than the obvious alternative, the production of carriers, especially in perennial plants or those propagated vegetatively. The use of carrier varieties is undoubtedly of value in reducing losses from any particular virus, but the practice is full of dangers. With a carrier variety it is impossible to practise roguing, so that infected plants remain as permanent sources of infection and the whole stock becomes infected. Thus, if carrier varieties are at all widely grown enormous reservoirs of virus may be built up. This may be of little importance if the host range of a virus is limited to one crop, all varieties of which are carriers, but if the virus has a wide host range or if varieties differ in their tolerance (as, for example, in strawberries, raspberries or potatoes) the dangers of such carriers will be obvious.

Virus Strains and Mutation

There is another objection to the use of carrier varieties. So far we have talked of individual viruses as though they were fixed, unchanging entities, but this is far from being true. Most of our common viruses are now known to exist in strains or variants with different pathological propensities, and, in many of them, changes akin to mutations occur with disconcerting frequency. The chances of a variant being produced will, other things being equal, depend on the number of individual virus particles produced, and this, of course, is greatly increased if infected carriers are widely grown. Stocks of many of our widely grown potato varieties such as Majestic and Arran Banner, are fully infected with potato virus X. The best stocks are infected with strains which they can carry, whereas the poorer stocks contain strains that produce obvious symptoms. To keep stocks of the highest commercial quality it is necessary to remove each year plants that show mosaic symptoms. Such plants are not, as is generally thought, always the result of new infections, but are often caused by the segregation of a more virulent variant from the virus that was previously carried.

So many viruses have been found to occur in strains, and some individual viruses in so many different strains, that it is impossible here to deal with them in any detail. Different strains, however, may cause such dissimilar symptoms in the same plant that from the appearance of the plants alone one would not suspect any relationship. Indeed, many viruses that are now known to be related strains were originally described as separate viruses under different names. In general, we can say that strains of one virus have similar chemical and physical properties, but differ in the type of symptom they cause in one or more plants. For example, with tobacco mosaic virus in tomato, one strain produces a mild green mottling, a second produces bright yellow mosaic, a third is responsible for fern-leaf symptoms, and a fourth gives necrosis.

Similarly, with potato virus X in the variety Majestic, symptoms vary from a lethal top-necrosis, through crinkles with scattered necrosis to a mild mosaic or to no obvious effects, depending on the particular strain employed.

The study of variants of viruses has led to the discovery of the first authentic examples of acquired immunity known in plants. When a plant is already infected with one strain of a virus it is protected against further infection with other strains to which healthy plants of the same species are susceptible (Fig. 7). As the infected plants still retain their susceptibility to other unrelated viruses, this fact gives a useful method of testing relationships between viruses that cause different symptoms. To determine whether a virus causing a new type of symptom in, say, tomato is a strain of tobacco mosaic or cucumber mosaic virus or is distinct from both, it is only necessary to inoculate the unknown virus to plants previously infected with each of these, and see which develops new symptoms. If both do, the unknown one is distinct from both, if only the one with tobacco mosaic does, then it is a cucumber mosaic virus, or *vice versa*. The mechanism underlying this acquired immunity is unknown. If two strains of one virus enter a healthy plant simultaneously, both multiply. The two, however, often segregate into different regions of the same leaf, and by selecting for inoculum portions showing different symptoms, apparently pure cultures of each strain can be recovered. The protection therefore is clearly not an inactivating effect of one strain on another. It seems probable that there is a limiting amount of any one virus that a cell can produce, and if one strain has already multiplied to this extent a second is unable to become established. The protection extends only to tissues that are infected with one strain and its extent depends on the virus concentration in the plant. The phenomenon superficially resembles the vaccination of animals, but again, there is no evidence of antibody production in the plant. It is worth noting, however, that the virus strains which protect plants against one another do also share antigens.

Strains of a number of common viruses are known which produce only slight effects on their economically important hosts. This suggests the possibility of protecting crops against the losses caused by virulent strains by deliberately infecting the plants early in life with avirulent strains. Until tests have been made, judgment cannot be passed on its practical possibilities, but there are serious objections to the method. First, virulence is often merely a reflection of a host-parasite relationship and not a fundamental property of the parasite itself. A virus may be avirulent in one host but virulent in another, so that by protecting one crop dangerous infection-foci for other crops might be established. Secondly the possibility of new variants which might be virulent towards either the " protected " crop or some other would be a continuous risk. A third, and more serious, disadvantage is the possibility of the protected plant becoming infected wih an unrelated virus, for such a double infection often has disastrous results (Fig. 8). Two avirulent strains of unrelated viruses may produce a worse disease than a virulent strain of either virus alone. Many strains of potato virus X, for example, have little serious effects on tomato, but if they infect plants " protected " by previous inoculation with a mild strain of tobacco mosaic virus, they cause a serious necrotic disease.

Internal Symptoms

The internal changes produced in plants by virus infections can be considered under two headings ; first, there are modifications of normal tissues and second, the production of new structures, the specific intracellular inclusion bodies. Some of the first types of internal change merely reflect the external symptoms. Sections of mottled leaves show that the chlorotic regions are thinner than the green while the plastids are smaller, more granular, less deeply coloured, and often have more irregular outlines. Although there is this reduction in the assimilatory tissues, there is often an abnormal accumulation of starch in cells of chlorotic leaves. This is found in many diseases of the yellows type and is particularly true of potato leaf roll, in which the chloroplasts of rolled leaves are often so full of starch that they burst. In this type of disease, there is often necrosis of the phloem leading to the collapse of sieve tubes and companion cells. With diseases in which external symptoms are of the necrotic type, corresponding microscopical changes also occur. In top-necrosis of the potato, which can be caused by several different viruses and virus strains, a necrosis starts in the phloem, from which it may spread to affect all other tissues. In leaf-drop-streak, caused by potato virus Y, on the other hand, necrosis starts in the mesophyll of the leaves and spreads down the petioles to the main stem, where the corti-

cal tissues die, but the vascular tissues are unaffected. An unusual symptom, failure of the wood to become fully lignified, has been described in the condition known as rubbery wood of Lord Lambourne apples. This shows itself in the unusual elasticity of the branches which can be bent and twisted to a remarkable extent without breaking.

Peculiar intracellular inclusion bodies were known to accompany some diseases of animals long before the existence of viruses was recognised. The association of these inclusions with virus diseases became evident in 1902, when two kinds were described in the cytoplasm of plants suffering from tobacco mosaic. The first was an amœboid-like, amorphous body (Fig. 9) and the other crystalline (Fig. 10). Since then analogous bodies have been described in many different virus diseases, in some occurring with sufficient frequency to be of diagnostic value. Such bodies seem to be absolutely characteristic of virus diseases, for they have not been seen in either healthy plants or in those suffering from any other type of disease. Thus, if such bodies are found one can be fairly sure that one is dealing with a virus disease. The converse, however, does not hold, for not all viruses cause their production; also, in some virus diseases inclusions are produced only sparsely, and, in others, they persist for only a limited period.

Until recently attention was concentrated mainly on the amorphous inclusions, for most workers agreed that the crystals were merely plant reaction products, but opinion was divided as to their etiological significance. Some workers thought these bodies also were merely cell reaction products, while others thought that they were stages in the life cycle of an organism responsible for the disease, and such properties as autonomous movement and multiplication by fission were attributed to them.

A detailed study of the method whereby these bodies were formed helped to explain much that was previously obscure and pointed out a connection between the amorphous and crystalline inclusions produced by tobacco mosaic virus. Soon after cells become infected the rate of cytoplasmic streaming is increased and abnormal granules can be seen circulating. These are carried passively around the cell and when they meet they fuse to produce larger aggregates. This process of fusion continues until all the granules are contained in a single body, which also often contains mitochondria, oil globules and other substances acquired during circulation round the cell. The fully formed vacuolar body persists for about a month when it begins to disintegrate, often first changing into crystalline material indistinguishable from that of the ordinary crystalline inclusions. The amorphous bodies are relatively stable, though they are disrupted by pricking. They have been removed from infected cells, dissolved and found to contain considerable amounts of virus, for they are approximately as infective as estimated equal weights of purified virus.

The crystalline inclusions are very variable in shape and also extremely fragile. If the cell containing them is injured or if acid is added, as when fixing, they disintegrate, first producing needle-like fibres resembling precipitated purified virus, and then going into solution. Some are undoubtedly true crystals for they are perfect hexagons, and as they turn over in the sap they show both side and end facets. They are birefringent when viewed edgeways in polarised light, but not when viewed flat. Others have less regular outlines and look like crystalline aggregates, while sometimes the inclusions take on a variety of different fibrous forms.

Different viruses give rise to slightly different kinds of inclusions and produce them most abundantly in different tissues. Those caused by tobacco mosaic are chiefly found in the epidermal tissues, potato virus X produces them mainly in the palisade and spongy parenchyma, and in curly top of sugar beet they are restricted to the phloem, whereas tobacco etch virus produces them in all parts of infected plants. The most general type is the cytoplasmic type of amorphous inclusion, but a number of viruses other than tobacco mosaic also produce crystalline or fibrous inclusions. In addition to cytoplasmic inclusions, tobacco etch virus causes the production of thin crystalline plates inside the nucleus (Fig. 11), and two viruses of leguminous plants cause the production of characteristic crystals in cytoplasm, nuclei and nucleoli.

The production of these inclusions can in part be simulated *in vitro* by precipitating purified viruses with various substances with which they combine to form insoluble complexes. It seems likely that the inclusions are analogous complexes, for we know they contain virus, but under the conditions of salt concentration and *p*H in cell sap virus should be in solution. Thus, although we cannot yet be certain, their etiological significance is

probably mid-way between the extreme views held earlier. The inclusions are neither the cause of the disease nor simple host reaction products, but are probably the visible results of a union between the virus and other specific constituents of infected cells.

Methods of Transmission

The three main methods whereby viruses can be transmitted from diseased to healthy plants are by grafting, by mechanical inoculation and by insects. Some viruses, such as potato Y and spotted wilt, have been transmitted by all three, whereas others have been transmitted by only one or two methods. Potato virus X and tobacco mosaic virus, for example, have been transmitted by grafting and inoculation but not by insects, potato leaf roll and sugar beet yellows by grafting and by insects but not by inoculation, whereas a large number of other viruses have been transmitted only by grafting. No doubt many of the last group do have other methods of transmission which will be discovered in further work.

Grafting is by far the most general method of transmission and is successful in transmitting all viruses between plants in which they cause systemic infections. Indeed, transmission by grafting has almost become the critical test of a virus disease. It is invaluable for research work and is also important practically, for there is no doubt that many diseases of fruit and ornamental trees and shrubs have become widely distributed by the original use of a few infected scions or stocks. It is likely that the unsuspected passage of viruses from scions to stocks has been responsible for many of the effects that have been attributed to the influence of scions on stocks. With viruses that give necrotic symptoms, systemic symptoms are often obtained by grafting whereas inoculation produces only local lesions. If *N. glutinosa* is grafted with scions taken from tobacco or tomato plants infected with tobacco mosaic virus, the plant dies with a systemic necrosis, whereas if leaves are inoculated only local lesions are produced. Similarly, potato viruses B and C give only local lesions when inoculated to certain varieties, but if these are grafted with systemically infected scions of other varieties, the viruses spread through the vascular system of the stock in which they cause a systemic lethal disease, top-necrosis (Figs. 12 and 13).

Transmission of some viruses has been achieved by linking diseased and healthy plants with the parasitic dodder (*Cuscuta* sp.). This effects an organic linkage between the plant analogous with that between scion and stock, but the union is not strictly comparable with grafting. Not all viruses can be transmitted by this method; some, such as aster yellows, bushy stunt and tobacco mosaic pass through the dodder fairly readily, but tobacco ringspot and pea wilt viruses do not. Failure to transmit does not seem to be restricted to viruses able to infect and multiply in the dodder, though these are transmitted more readily. It is improbable that this method of transmission is of any practical importance in spreading virus diseases, but it is interesting that dodder has been found naturally infected with a previously unknown virus and that the virus passed to a number of different plants when parasitised by the infected dodder. As a method of transmission, however, it promises to be of great value in research work with many different viruses now difficult to study because of pecularities of their host plants. The host range of viruses that cannot be transmitted by inoculation is restricted to species of plants that can be successfully intergrafted or on which the insect vector can feed. The use of dodder does away with this limitation, for by using different species of dodder unrelated plants can be linked. Already this has shown that some viruses, such as that causing cranberry false blossom, which were thought previously to be restricted to one host are in fact capable of infecting widely different plants.

In studying virus diseases it is important always to remember that two entities are concerned, the virus and the host plant. This has often been overlooked and phenomena that should have been attributed to one or the other have been interpreted as intrinsic properties of the virus. The methods by which a particular virus has been transmitted usually occupy a prominent part in its characterisation, because whether or not it has been transmitted by inoculation was regarded as a character of the virus, independent of the host. However, there is little doubt that this interpretation is often erroneous. Some viruses can be transmitted to some hosts by inoculation, but not to others. Potato virus A, for example, is fairly readily inoculated to tobacco, but not to potato, and dandelion, yellow mosaic virus to lettuce but not to dandelion. None of the viruses affecting strawberry or any other rosaceous plants has been transmitted by inoculation. This fact

ceases to be surprising when it is realised that all attempts to transmit such viruses by inoculation have been made with fluids that contained no virus. During maceration of the diseased leaves as a preliminary to extracting sap, much tannin is released which precipitates both the normal plant proteins and the viruses. Tannin is present in such quantities that if extracts of strawberry leaves are added to protein solutions, they cause precipitation ; they are also efficient inactivators of viruses like tobacco mosaic virus which are normally easy to transmit mechanically. It is, of course, possible that the strawberry viruses would not be transmissible mechanically even if they could be extracted from their host plant free from inactivating substances. This will remain untestable until they have been transferred to some host susceptible to viruses known to be transmitted mechanically. Until this has been done, failure of mechanical transmission can reasonably be regarded as a result of peculiarities of the host.

Uninjured plants are not susceptible to viruses, for infection occurs only though wounds. Wounding should not be severe, however, as viruses cannot multiply in killed cells. A light rubbing of leaves, sufficient to open the epidermal cells without causing any obvious damage, produces the best type of entry point. But there is still much that we do not know about the factors controlling infection. It seems probable that cells of different plants differ in the amount of virus required to cause infection. This would explain the fact already mentioned that inoculation with the same virus preparation sometimes gives infection in one susceptible host but not in another. It also seems likely that cells of different tissues of the same host plant may also vary in the initial dose of virus needed to initiate multiplication. A number of viruses which are normally difficult to transmit mechanically are readily inoculated if some suitable abrasive such as 500 mesh carborundum or celite is incorporated in the inoculum. By this method virus A can be inoculated to potatoes. If such abrasives are used with viruses that give countable local lesions, it is found that their effect is equivalent to increasing the virus content of a fluid by about a hundredfold (Table 1). It seems, therefore, that the normal failure to get transmission with potato virus A or dandelion yellow mosaic virus is because the virus content of sap from diseased plants is below that necessary for infection. As the addition of abrasives clearly cannot increase the amount of virus in the inoculum, it must act by reducing the resistance of the host plant. It may merely increase the total number of wounds, but it greatly increases the permeability of the leaf by stripping off the hairs and the waxy outer layer. In normal rubbing it is mainly the bases of the hair cells that are wounded and these may be more resistant to infection—that is more initial virus particles are needed to cause infection—than are the less superficial cells which are opened by abrasives.

Thus, two factors, a deleterious effect of expressed sap on the virus or a too small virus content in the sap, may explain why some viruses which are transmitted by insects are not also transmitted by inoculation. With other viruses it may be that they can only become established if placed directly in some specific, deep-seated tissue, such as the phloem, which is not penetrated by rubbing even if abrasives are used. Many viruses causing diseases of the yellows type cause abnormalities in the phloem and none of these has been transmitted mechanically except curly top of sugar beet, with which a few successes have been obtained by special injection methods designed to put the inoculum into the phloem. In this connection it is worth noting that the vectors of such viruses are all phloem feeders.

Transmission by Insects

In nature there is no doubt that the great majority of infections with viruses are the result of insect activity. The insects do not cause the diseases, they merely carry the viruses from infected to healthy plants. They do this, not merely by crawling over the plants and becoming contaminated externally, but by imbibing virus while feeding on an infected plant, and then ejecting it into healthy

TABLE I

Effect of Carborundum in Increasing Infectivity of Tobacco Mosaic Virus

Treatment	Average number of lesions per leaf at different virus concentrations				
	10^{-5}	10^{-6}	10^{-7}	10^{-8}	10^{-9}
Carborundum in inoculum	407	166	26	5	1
No carborundum	24	4	2	0	0

plants on which they feed subsequently. Vectors of viruses are insects with sucking mouth-parts, and there are very few authenticated records of transmission by biting insects. The main types of insect involved in virus transmission are leaf-hoppers, plant bugs, white-fly, thrips and aphides, but the aphides are by far the most important and are responsible for the transmission of more viruses than all other types of insect combined. Of the viruses in Britain known to be insect-transmitted, all have been found to have aphides as their vectors except tomato spotted wilt, which is transmitted by thrips, and reversion of black currant, which is probably transmitted by the big-bud mite.

Two contrasting types of relationships have been distinguished between different viruses and their insect vectors. Vectors of one type of virus can infect a healthy plant immediately after they have fed on a diseased plant, and such vectors usually cease to be infective within a short time, usually within a few hours, of leaving the infected plant. Vectors of the second type cannot infect healthy plants immediately after they have fed on a diseased plant; there is a delay in the development of infectivity, sometimes called an incubation period, which with different viruses varies from hours to days. Once such vectors have become infective, they remain so for long periods, sometimes for the whole of their lives. For long it was generally accepted that viruses of the first type were transmitted in a simple mechanical manner as contaminations on the outside of the vectors' mouth-parts, whereas the second type were thought to have some obligate relationships with their vectors. Indeed, it was believed that the incubation period is a time during which such viruses either undergo some developmental change or multiply sufficiently for the insect to become infective. There is no positive evidence for either of these views.

If the viruses that do not persist for long in their vectors were carried mechanically as contaminants on the stylets, then it would be reasonable to expect that all insects with similar feeding habits would be equally efficient as vectors, and that the viruses most easily transmitted mechanically would be the most easily transmitted by insects. The truth is the reverse of this. Potato virus X and tobacco mosaic virus occur in high concentration in infected plants, and are the viruses most readily transmitted mechanically, but they are not transmitted by insects that are vectors of other viruses. From plants that are simultaneously infected with mixtures of tobacco mosaic and cucumber mosaic viruses, tobacco mosaic virus alone will be transmitted by needle prick whereas aphides will always transmit only cucumber mosaic virus. There is also considerable specificity in the viruses that individual insects can transmit. An example of this is given in Table 2, where the abilities of a newly-described aphis and of the peach aphis to transmit several viruses are compared. It will be seen that two aphides may both transmit one virus, while other viruses are transmitted selectively by one or other of the aphides. Another feature of the transmission of many non-persistent viruses that tells against a simple mechanical interpretation, is that the ability of vector species to transmit is greatly affected by their activities before feeding on a diseased plant. If the vectors have not fed for an hour or so before being transferred to the diseased plant, they may give more than five times as many transmissions as vectors that have fed continuously. This effect, however, is obtained only if the vectors feed for short periods on the source of the virus, preferably for only a few minutes. If the period of feeding on the infected plant is prolonged, vectors become less efficient, though the chances of acquiring additional virus are obviously increased. It is clear that

TABLE 2

COMPARATIVE TRANSMISSION OF DIFFERENT VIRUSES BY THE PEACH APHIS AND THE SHALLOT APHIS

Virus	*Peach aphis*	*Shallot aphis*
Potato Y	*19/20	0/47
Cucumber mosaic	18/20	41/50
Hyoscyamus 3	10/10	20/35
Severe etch	10/10	0/30
Lettuce mosaic	24/24	0/38
Sugar beet mosaic	10/10	0/10
Dandelion yellows mosaic	0/30	7/33
Sugar beet yellows	10/10	5/10

* Numerator is the number of plants infected, denominator number colonised. For any one virus, the number of individual insects used per test plant was the same for both species of aphis.

the act of continuous feeding, whether on an infected or healthy plant, has a deleterious effect on the virus. The reason is unknown, but the simplest explanation is that while feeding the insects secrete substances that inactivate this type of virus.

Not all the vectors of non-persistent viruses show this increase in efficiency as a result of a preliminary period without food. Vectors of dandelion yellow mosaic virus always lose their infectivity within an hour of leaving a diseased plant, yet they give no more transmissions if starved before their infection feeding. This may be explained by the low virus content of the infected plants, as the virus is one that is transmitted mechanically only when infective sap is inoculated with added abrasive. The aphis vector of this virus needs to feed for at least an hour on infected plants before it becomes infective, probably because it takes this time to acquire enough virus, and during this necessary feeding period the beneficial effects of a preliminary fast have probably been lost. With viruses such as potato Y and tobacco etch, the position is very different as the aphis can become infective with feeding periods of less than one minute. This shows how much more efficient is the aphis at causing infection than are mechanical methods of inoculation. To infect healthy tobacco plants they must be rubbed with the equivalent of about 1/1,000 of a cc. of infective sap, whereas in a feeding period as short as one minute an aphis imbibes much less than this.

All the non-persistent viruses so far studied have been found to be transmitted by aphides. The vectors of persistent viruses are less homogeneous, different viruses of this group having leaf-hoppers, white-fly and thrips, as well as aphides as their vectors. That the difference in behaviour is determined by the virus and not the insect, is shown by the fact that some species of aphides transmit both types of virus. Many workers believe that these viruses multiply in their insect vectors ; they interpret the latent period in the vector as equivalent to the time between infection of plants and the production of symptoms, and attribute the prolonged retention of infectivity to constant production of new virus in the vectors. There is no *a priori* reason why plant viruses should not multiply in their insect vectors and the theory would conveniently explain many observed phenomena. Unfortunately no critical experiments have been made to test the theory, and the evidence advanced in support of it can all be interpreted in other ways. Many vectors, for instance, lose infectivity, which they would not be expected to do if the virus was multiplying in them, and the evidence there is indicates that the vectors never contain more virus than they acquire while feeding on diseased plants. The number of plants they can infect, and the length of time they remain infective, seem to be determined by the length of time they have fed on infected plants. Also, though on this point there is little direct evidence, it seems that the latent period begins not from the time the vectors first begin to imbibe virus by feeding on a diseased plant, but from the time they leave the plant and begin to feed on healthy ones. The viruses have no apparent ill-effects on their vectors : infective insects live as long and breed as freely as non-infective individuals. With one exception, it has been found that infective adults do not pass on the viruses to their progeny. The exception is the leaf-hopper that transmits dwarf disease of rice, in which progeny up to the seventh generation have been found to be infective, and the progeny from one single egg infected more than 1,000 individual plants without having recourse to feeding on a diseased plant. This is put forward as the strongest evidence of virus multiplication, but again is far from conclusive. Vectors of rice dwarf virus often cease to be infective, suggesting that they cease to contain virus, a fact that conflicts with the theory of multiplication. It is possible that the injection of a single virus particle by the vector leads to infection in plants, so that for the maximum number of infections obtained one need postulate that the original insect imbibed something over 1,000 virus particles while feeding on a diseased plant. This would probably weigh no more than about 10^{-14} gms., an amount that would be inconsiderable even in the minute egg of a leaf-hopper.

When one sees the vast infestations of insects that commonly occur on crops and remembers the simple phrase that " viruses are transmitted by insects," at first sight it seems impossible that any plants should escape infection. The reason they do is that certain very definite conditions must be fulfilled before viruses are transmitted, and the great majority of insects never fulfil them. First, the right species of insects must be present ; for most individual viruses are specifically transmitted by only one, or by a few closely related, species. Secondly, there must be a source of the virus, for the vector

must feed on an infected plant before it can infect a healthy plant. But, as we have already seen, even when the vectors are present and feed on infected plants their ability to transmit depends on the conditions of feeding. Some viruses are transmitted readily only if their vectors arrive on the diseased plant after a period without food, stay only momentarily, and then move to a healthy plant, and unless such vectors again feed on an infected plant they soon cease to be infective. Other viruses are transmitted only if their vectors feed for prolonged periods on diseased plants; vectors of such viruses do not become infective immediately, so that the first healthy plants on which they chance to feed may fail to become infected. There are also additional, specific conditions to be fulfilled before some individual viruses can be transmitted. The vector of spotted wilt virus, for example, can only become infective if it feeds on a diseased plant while it is still in the larval stage. Adults can infect healthy plants if they have acquired the virus when they were larvæ, but they cannot themselves become infective by feeding on diseased plants. Also two viruses have been studied which are transmitted by certain species of aphides only when they occur together with another insect-transmitted virus. Potato virus F, for example, is not transmitted by its vector except in conjunction with potato virus A; similarly, aphides cannot transmit tobacco mottle virus from plants infected with this virus alone, but they can transmit it from plants infected simultaneously with tobacco vein-distorting virus. Thirdly, for transmission to occur, insects must be moving about. Those that spend their whole lives on a single plant do no spreading of viruses. This fact may explain why aphides that have been found to be excellent vectors in glasshouse experiments, sometimes seem to be inefficient in the field. It may also explain the great importance of the peach aphis, *Myzus persicae*, as a vector in the field.

When compared with *M. persicae* experimentally, *Aphis rhamni* is found to be equally good as a vector of potato virus Y, but in the field infestations of thousands of *A. rhamni* often give little or no spread whereas a small infestation of *M. persicae* can often spread the virus widely. Similarly, the black aphis, *Aphis fabae*, is, in glasshouse tests, almost as efficient as *M. persicae* in transmitting yellows and mosaic of sugar beet, yet often in fields that are black with aphides there is little virus disease, whereas in those with relatively slight infestations of *M. persicae* the plants are often all infected. In experimental work, the aphides are placed on the infected plants, and then moved from these to healthy plants. In nature, however, such movement depends on the behaviour of the particular insect and, whereas *M. persicae* seems to move freely, for it usually produces fairly uniform infestations over a whole crop, *A. rhamni* and *A. fabae* do not, for they often give dense local infestations. Another feature of *M. persicae* that makes it of great importance is its ability to feed on a wide range of host plants, so that its chances of acquiring viruses are much larger than those of aphides which can feed and breed on only a limited number of plant species.

Factors Affecting Spread in the Field

We have seen that before healthy plants can become infected with insect-borne viruses there must be present both infected plants and the specific insect vector, which, to function, must be moving from plant to plant. Clearly for the control of such diseases, there are three possibilities; remove sources of infection, destroy the insects or prevent them from moving. The first is, of course, a general control measure for all infectious diseases, and should always be practised; it is rarely possible, however, to achieve 100 per cent. success, and roguing against virus diseases is often complicated by the occurrence of symptomless carriers. There are also recognised methods of dealing with insect infestations, but treatments that are successful in dealing with insects as pests are not necessarily successful in preventing the spread of viruses. Under glass, fumigation can rid houses of insects, and this is a most valuable safeguard against such viruses as tomato spotted wilt and cucumber mosaic viruses. But in the field little success has so far attended the use of insecticides used as sprays, dusts, or as fumigants, in attempts to control virus diseases. To control an insect pest, it is only necessary to reduce the number of insects below the level at which direct damage is caused to the crop, but this may not be enough to stop the spread of viruses. Indeed, if most of the insects are killed by a treatment, but the few remaining are disturbed so that they become restless and are stimulated to move from plant to plant, the treatment may do more harm than good. Also, if transmission is largely a result of the activities of winged migrants entering the crop, much spread may occur before the crop shows sign

of being infested, and the need for treatment becomes obvious. The testing of insecticides against virus diseases, however, is only yet in its infancy and the future may be brighter than past results would indicate. The discovery of a really effective deterrent for *M. persicae*, for example, would represent a great advance. Meanwhile, the use of existing insecticides may prove valuable against such aphides as *Capitophorus fragæfolii*, the vector of strawberry virus diseases, which produces winged forms only once a year, and is restricted to one host.

As the spread of most viruses is determined by the activities of their insect vectors, it will be clear that the injury to crops will be determined by weather conditions that affect the vectors. Some of these conditions will affect different insects differently, and our knowledge of this subject is still far from complete. The effects of varying conditions, however, have been studied with *M. persicae* and we know something of the factors that influence its behaviour. It does not fly at all readily if the temperature is below 65° F., the relative humidity over 70, or if there is a wind of more than eight miles per hour. Thus, when these conditions prevail there will be little movement of the aphides or spread of virus. The infestations of potatoes, sugar beet brassicæ and other hosts of this aphis will depend on the magnitude and date of the spring migration. This in turn will depend on the type of weather experienced during both the winter and early spring. The normal method whereby *M. persicae* overwinters is in the egg stage on peach trees. The eggs hatch in early spring and there are several generations of wingless aphides before the winged forms are produced and migrate to the summer hosts. In a warm spring, the aphides will develop more rapidly than during cold weather.

If the winter is mild the aphis has an alternative method of overwintering, without recourse to the egg-laying stage on the peach. It can continue to live throughout the winter producing living young on brassicæ or sugar beet seed crops. Should a warm spring ensue, these also multiply rapidly and produce winged forms able to move to other crops when weather conditions are suitable for flight. It will be apparent that this type of overwintering is particularly likely to lead to spread of virus diseases. All the aphides coming from the peach will be free from viruses that affect the summer host plants of *M. persicae* until they have fed on a diseased plant in the course of their travels. Aphides that have overwintered on brassicæ or sugar beet seed crops, however, may start migration already infective, and if they move from one brassicæ crop to another, or from a sugar beet seed crop to a root crop, they may introduce viruses immediately. Thus, although the subject is too complex for such a simple analysis to be more than an approximation to the whole story, we can say that after a severe winter, especially if followed by a cold spring and wet or windy weather when the winged migrants are developing, there will be little spread of viruses relative to that after a mild winter and a warm spring.

The control of potato virus diseases by the regular purchase of new stocks of seed potatoes depends on such effects of climate in determining the rate of spread of virus diseases. In the south and east of Britain, stocks of potatoes rapidly degenerate so that within two or three years their yielding capacity may have fallen to less than one-half of the original. In such districts losses are avoided by regularly obtaining new stocks of seed tubers from the north and west, mainly from Scotland. In recent years English farmers have purchased annually nearly 500,000 tons of seed potatoes from Scotland, nearly enough to plant half the total acreage of potatoes in England. The virtues of the newly-imported seed have been mainly attributed to a beneficial effect of "change of soil," though this manifestly ignores the fact that the same stocks have been grown continuously for many years on the same farms in Scotland without degenerating. The differences between those districts that produce good seed and those that do not are climatic, the conditions in the first being such as to discourage the multiplication and movement of *M. persicae*. In the regions of Scotland which produce the best seed potatoes, there are few peach trees or overwintering brassicæ crops, so that the numbers of aphides about early in spring are few. The spring weather is far from ideal for rapid multiplication and the dry, warm windless days favourable for migration are rare. Aphides therefore do not reach the potatoes in large numbers early in the growing season as they do in the ware-growing districts of England, where there are abundant overwintering hosts of *M. persicae*, and the spring weather is more favourable for multiplication and migration. There is a further fact that explains the superiority of Scotch seed. Where there is little spread of virus diseases, it is relatively easy to get rid of sources of

infection by roguing out affected plants. This the Scottish farmer has done over a period of years so that, even if conditions in any year become especially favourable for aphides and a heavy infestation occurs, not much damage results, as there are few sources of virus from which spread can occur.

The principle of growing special certified stocks for seed purposes, which has proved so successful in controlling potato virus diseases, is now being extended to other crops that are propagated vegetatively. This is to be welcomed because it seems the most likely method of producing dependable planting material; provided such stocks are isolated from other commercial stocks of the same species and they are rogued and inspected, it should not prove difficult to maintain their health and vigour. The conditions that have proved limiting for the spread of virus diseases of potatoes are those that adversely affect *M. persicae* and there is no reason to assume that these will be equally limiting factors for other aphides. For example, the potato crop starts each year free from aphides, and if one season should be favourable and lead to an infestation, the effects are only temporary. With other crops, however, a single year favourable for aphides may lead to more lasting results. The strawberry aphis, for example, spends its whole life on the strawberry plant, and, if aphides reach isolated plots during conditions favourable for migration, they will persist through the winter and increase when conditions are suitable. With such perennial plants having autœcious insects as vectors of viruses, it is obvious that additional precautions may be needed to those found effective for producing good seed potatoes.

Transmission by Seed

So far we have considered only the methods whereby viruses spread from infected to healthy plants, although their perpetuation by vegetative methods of propagation has been implied repeatedly. Except in experimental conditions, we have seen that it is usual for viruses to spread throughout the vegetative parts of the host plants in which they persist for as long as the plants remain alive. Thus in perennial plants, or in those propagated vegetatively, the survival of viruses from year to year is simply explained, for the viruses will be contained in dormant tissues and in such vegetative organs of reproduction as tubers, bulbs, rhizomes, and the like. For unknown reasons, however, it is rare for viruses to pass into either pollen grains or ovules, and seed taken from virus infected plants usually gives rise to healthy plants. It was early noted that such plants as potatoes grew vigorously when first raised as seedlings, but soon lost their cropping power if propagated from tubers. This gave rise to the widespread belief that asexual reproduction is "unnatural" and leads to degeneracy which can be prevented only by the more "natural" method of sexual reproduction. There is, in fact, no evidence to favour the view that one method of reproduction is any more deleterious than another. The differences arise merely because the longer a stock is propagated vegetatively the more chance it has of becoming virus-infected, and whereas all the viruses it acquires will be perpetuated by vegetative methods of reproduction, they will be eliminated by the use of seed. Provided plants are kept free from virus diseases there is no evidence that their cropping power is in any way affected by vegetative methods of propagation.

As with all generalisations about viruses, there are exceptions to the statement that viruses are not seed-transmitted. Some are. The most important of these are the viruses of leguminous plants, and as many as 50 per cent. of the seeds set by infected broad beans, peas and French beans may give rise to infected seedlings (Fig. 14). Another exception is lettuce mosaic virus: this is regularly seed-transmitted, and about 3 per cent. of seed taken from infected plants usually produces diseased seedlings. It is possible that viruses of some other plants, such as cucumber, are also very occasionally seed-transmitted, but with viruses of most crops it has been repeatedly demonstrated that seed taken from infected plants gives virus-free seedlings. Nevertheless, it is good advice to take seed from healthy plants whenever possible, for seed from infected plants is often poorer in quality and germination. Also, the presence of some viruses, such as tobacco mosaic and severe etch, has been detected in the coats of seeds whose embryos were not infected and which germinated to give healthy plants.

Except for legumes and lettuce, therefore, it is rarely justifiable to blame the seed merchant for the viruses that regularly attack our plants raised annually from seeds. The sources of infection are usually local. For viruses such as cucumber mosaic and spotted wilt, which have wide host ranges, the sources are usually perennial or vegetatively propagated hosts, often ornamentals or weeds.

FIG. 1.—*The stunting produced in broccoli by infection with cauliflower mosaic virus. Photograph taken in May ; left-hand plant infected in previous summer, right-hand plant healthy.*

FIG. 2.—*Upper part of tomato plant infected with cucumber mosaic virus, showing the condition known as fern-leaf in which the leaves are much deformed and reduced in size.*

FIG. 3.—*Breaking in wallflowers. Left-hand plant showing streaking of petals caused by infection with cabbage ringspot virus ; right-hand plant healthy.*

FIG. 4.—*Leaf from Majestic potato suffering from leaf drop streak, caused in the first year of infection with potato virus Y. In subsequent years,* i.e., *when infected tubers are planted, the disease caused is severe mosaic* (*see Fig.* 5).

FIG. 5.—*Virus diseases in Majestic potatoes. Left-hand plant, severe mosaic, second-year infection with potato virus Y; centre plant leaf roll; right-hand plant healthy.*

FIG. 6.—*Tobacco plant photographed six weeks after infection with a ringspot virus. The plant has recovered, and the upper leaves look normal, though they still contain the virus, while necroses can be seen on the lower leaves.*

FIG. 7.—*Acquired immunity in* Datura stramonium. *Two leaves as they appeared six days after both were inoculated with a virulent strain of potato virus X. The right-hand leaf was healthy at the time of inoculation and shows severe necrosis. The left-hand leaf was infected with an avirulent strain of virus X (the faint mottle this causes is barely perceptible) and is protected against the virulent strain.*

FIG. 8.—*Tomato streak produced by simultaneous infection with potato virus X and tobacco mosaic virus. Left-hand plant infected with a mild strain of potato virus X; centre plant infected with both viruses; right-hand plant infected with a mild strain of tobacco mosaic virus. Photograph taken 14 days after infection.*

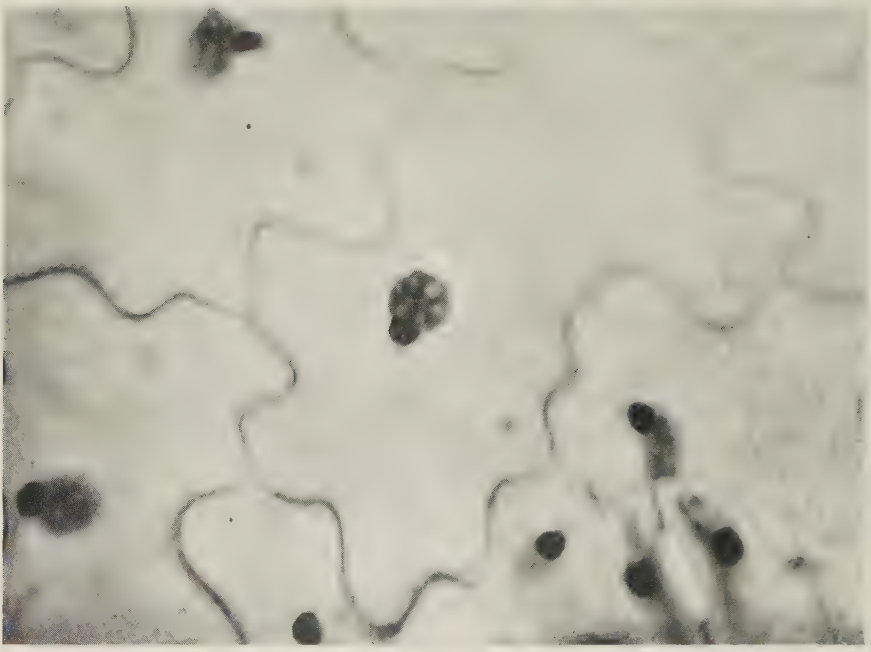


FIG. 9.—*Epidermal strip of* Solanum nodiflorum *infected with a strain of tobacco mosaic virus, showing the vacuolar inclusion bodies in contact with the smaller, more darkly-stained nuclei.* x 480

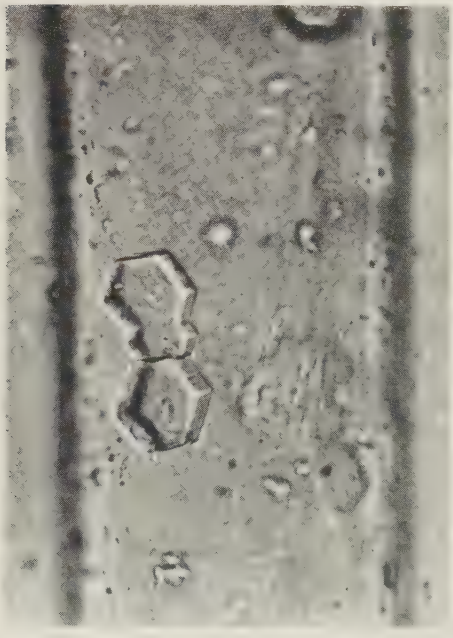


FIG. 10.—*Hair cell of tobacco infected with tobacco mosaic virus, showing two plate-like crystalline inclusions, one being almost a perfect hexagon.* x 450

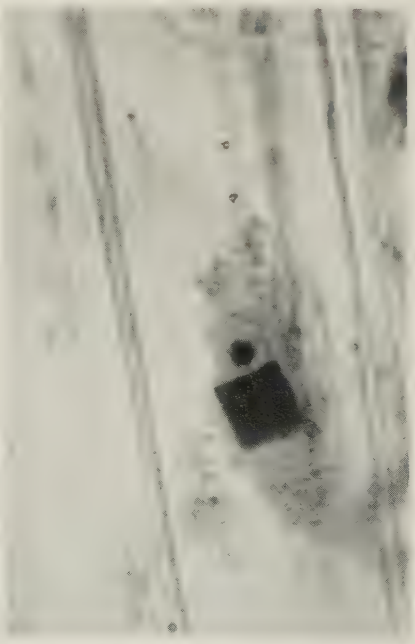


FIG. 11.—*Epidermal cell from a tobacco leaf infected with mild etch virus, stained with hæmatoxylin and showing a nucleus containing a single large, crystalline inclusion body.* x 900

FIG. 12.—*Leaf of President potato inoculated with potato virus B, showing necrotic local lesions, the only symptoms produced by this method of transmission (see Fig. 13).*

FIG. 13.—*President potato plant grafted with a scion taken from a carrier variety infected with potato virus B. The small side shoots of the stock are dying from top-necrosis,*

FIG. 14.—*Mosaic in French bean* (Phaseolus vulgaris, *var. Canadian Wonder*). *Centre leaf from healthy plant; others from diseased plants produced from infected seed.*

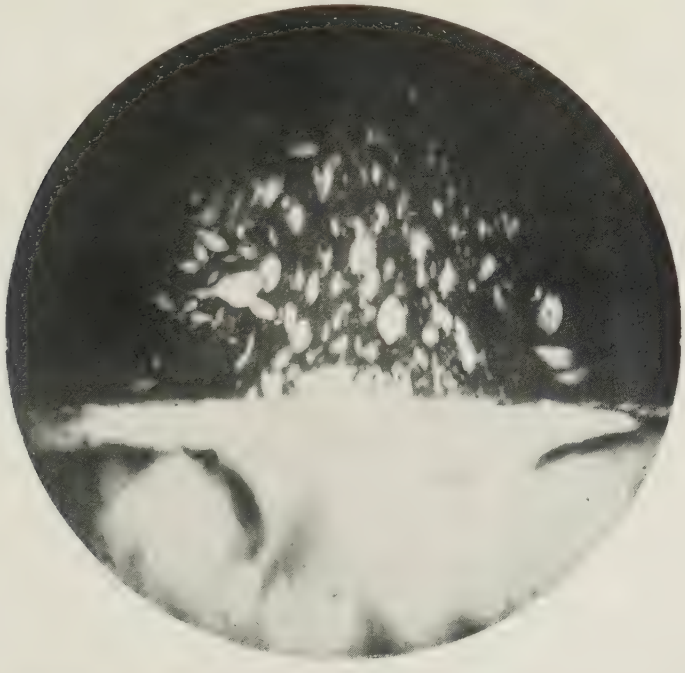


FIG. 15.—*The formation of a liquid crystalline layer in solutions of purified tobacco mosaic virus. Photomicrograph, in polarised light, of the interface between top and bottom layers in a fluid that had stood undisturbed for six hours. Most of the upper layer is not birefringent, but contains birefringent spindle-shaped tactoids, which are slowly settling into the liquid crystalline lower layer.*

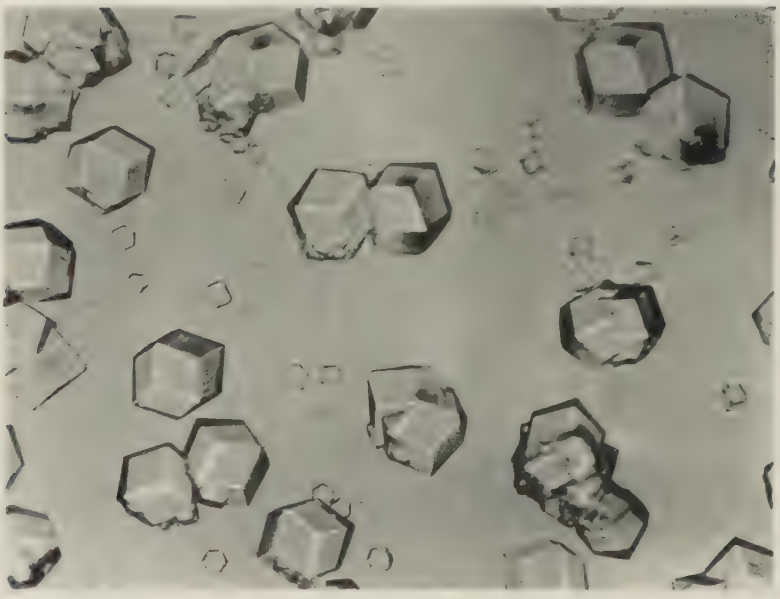
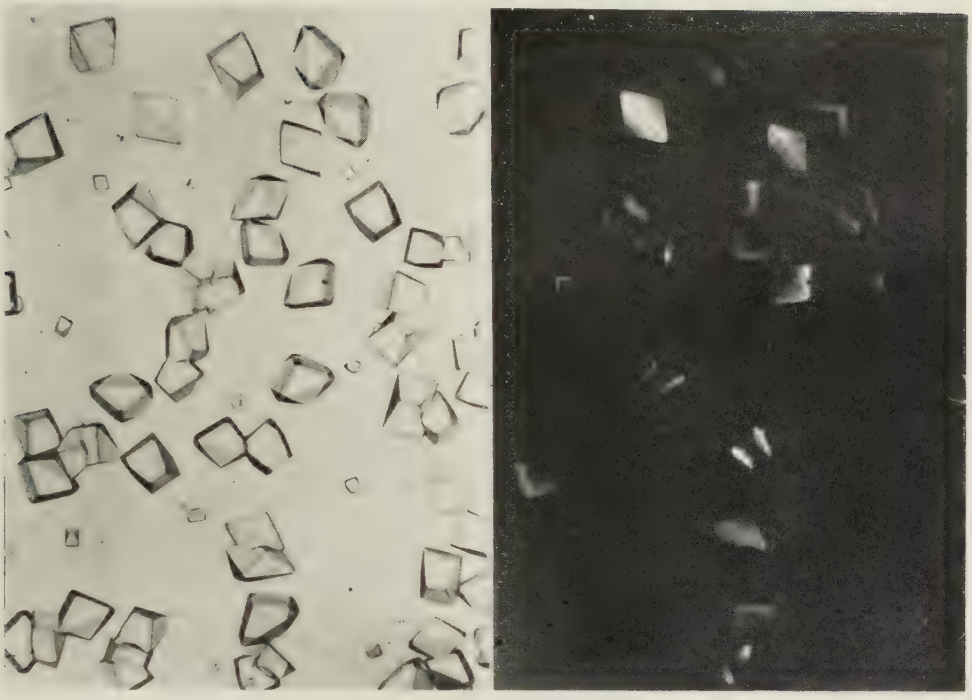


FIG. 16.—*Dodecahedral crystals of tomato bushy stunt virus, produced by slow precipitation with ammonium sulphate in the cold.* x 250

FIG. 17.—*Tobacco leaf suffering from tobacco necrosis. The symptoms consist of necrotic local lesions and can be produced by several distinct viruses. The opposite halves of this leaf were rubbed with serologically unrelated viruses.*



A B

FIG. 18.—*Birefringent bipyramids produced by the crystallisation of a tobacco necrosis virus. A, photographed in ordinary light, B in polarised light.* x 80

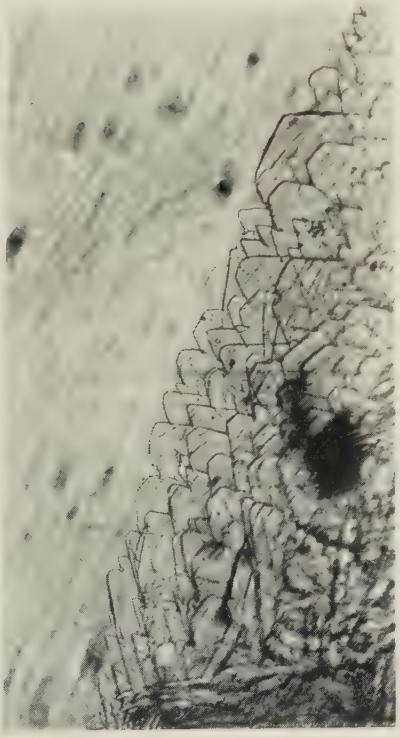


FIG. 19.—*The serrated edge of a crystalline pellet produced by sedimenting the Rothamsted tobacco necrosis virus in*

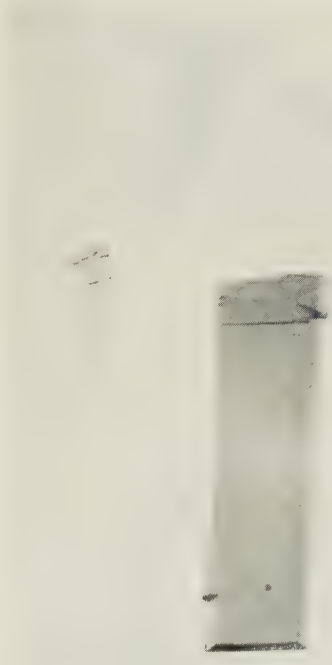


FIG. 20.—*Crystals of the Rothamsted tobacco necrosis virus produced from salt-free solutions in which crystal growth had*

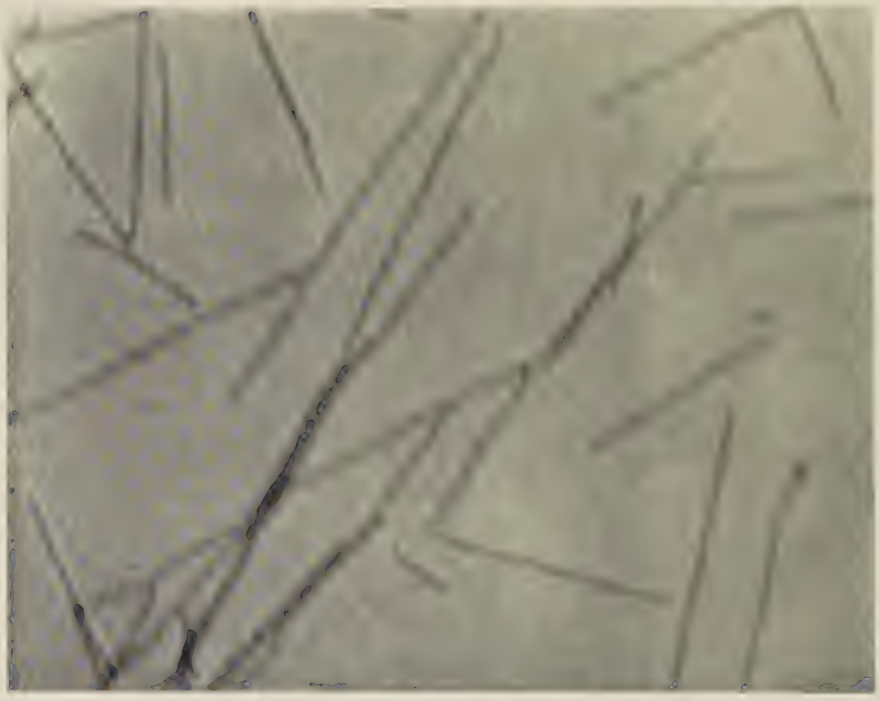


FIG. 21.—*Electron micrograph of a dried film of purified tobacco mosaic virus, showing rod-like particle of various lengths.* x 48,000.

For viruses with more restricted host ranges, the sources will be related plants to those that suffer. Viruses attacking cruciferous plants are perpetuated through the sequence of brassicæ that covers the gardeners' year; some types, for example, brussels sprouts, are in the ground for much of the year, and, as other types overlap, there is ample opportunity for the aphides to move from a maturing type to a succeeding newly-planted one. The viruses that have been so widespread in sugar beet in recent years survive the winter mainly on the stecklings grown to provide the succeeding year's seed crop. By separating the steckling beds from the root crop, this disease could probably be much reduced, though garden crops such as spinach beet, which stand through the winter are also often infected. One of the commonest viruses, tobacco mosaic, which is almost universal throughout our commercial tomato houses, is probably perpetuated in a different way, though there is little conclusive evidence about the method whereby each year's crop becomes infected. This virus is outstanding in its stability; it survives heating to 90° C. or drying, and retains infectivity for many years in infected plant tissues. It seems probable that most of the attacks of this virus originate from debris of infected plants left in the soil, though some may come from contaminated samples of commercial tobacco. Only one plant per house needs to become infected from such a source to lead ultimately to all the plants becoming infected, for this virus is very readily transmitted from plant to plant, either by their rubbing together or by cultural operations which involve handling the plants.

The Purification of Viruses

In the early days of work on viruses, almost the only fact that was established with certainty was that they caused diseases. It was natural, therefore, that the study of viruses should have been left almost exclusively to pathologists. It is rather more surprising that this should have continued virtually unchanged for 40 years, because the main techniques of the bacteriologist and mycologist, the use of the microscope and culture media, are clearly ill-adapted to the study of entities whose chief characteristics are invisibility and inability to multiply *in vitro*. This period saw many great advances in our knowledge of such branches of the subject as symptomatology, methods of transmission, host ranges and variations in viruses, but it produced few results with a direct bearing on the precise nature of viruses. It was generally accepted that viruses were minute organisms, essentially similar to small bacteria, though there was no more positive evidence in favour of this view than for others, which were advanced at intervals, most often by workers on tobacco mosaic virus.

Within the last ten years, however, the techniques of the protein chemist have been increasingly used in work on viruses, and the results obtained necessitate considerable modifications of the earlier theories. As usual, the first advance came from work with tobacco mosaic virus, when in 1935 the claim was made that a crystalline protein had been isolated with the properties of this virus. Although the first description of this protein was far from accurate, it was soon confirmed that diseased plants do contain a specific and unusual protein, which there is every reason to believe is the virus itself. The work has been extended to plants infected separately with a dozen or so other viruses or virus strains, from each of which a characteristic protein has been isolated. The methods of purification will not be described here, but they are modifications and adaptations of those used for the purification of enzymes and other proteins. Purification is facilitated by selecting suitable starting material. Bean plants, for example, are less favourable than tobacco, because they contain a normal protein that is stable and sediments under many treatments together with the infecting viruses. Purification is easier with young than with old tobacco plants and is easier with plants grown during the winter than in the summer. The fragile leaves developed in winter contain few materials that interfere with purification, whereas the vigorous plants produced by greater light intensity and better growing conditions in summer contain large amounts of normal plant proteins and pigmented substances difficult to separate from the viruses. The general method of obtaining virus is to macerate infected leaves, extract the sap by squeezing through muslin, and then subject the sap to treatments that precipitate either the virus or the normal plant constituents, or to apply treatments that destroy these constituents but not the viruses. As viruses have larger particles than most normal proteins, sedimentation in the ultra-centrifuge affords a very useful method of fractionation and concentration. Except for potato X and alfalfa mosaic, all the viruses so far studied have been found to resist the action of trypsin,

and digestion with this enzyme is of great value in removing normal plant proteins ; indeed, there is evidence that tobacco mosaic virus preparations are rarely free from contaminants unless treated in this manner.

What evidence is there that the proteins isolated in this way are the viruses themselves ? There is a great deal, both direct and circumstantial, but there is also evidence that the processes of purification may lead to changes in the virus particles, so that the properties of purified preparations may differ from those of the viruses as originally produced in the plant. No such proteins have been found in virus-free plants, and the particular protein isolated is determined solely by the infecting virus. The quantity of protein that is obtained is directly proportional to the infectivity of the sap ; sap from tobacco plants suffering from mosaic is infectious at a dilution of 1 in 1,000,000, whereas the dilution-end-point of sap from plants infected with potato virus Y is 1 in 1,000. From a litre of the first about 2 grams of the purified protein can be obtained and from the second only 2 milligrams.

Before the proteins can be accepted as the viruses, evidence is needed on their infectivity. Infections have been caused by rubbing healthy plants with 10^{-10} of a gram of some purified preparations, but little though this is, it is still too much to assume that the preparations contain only one constituent. We can say, however, that if the protein is not the virus, then to account for this degree of infectivity the virus must be less complex and have smaller particles than the protein, for these certainly constitute by far the greater part of the preparation. Much emphasis used to be laid on the fact that loss of infectivity was closely correlated with conditions that led to denaturation of the protein, This is still true of many treatments applied to both tobacco mosaic and other viruses, and it is true that all gross changes in the proteins are accompanied by loss of infectivity, but there are a number of treatments known that destroy infectivity without producing any obvious changes in the physical, chemical or serological properties of the proteins.

Although non-infective preparations of the proteins can be made, no one has succeeded in getting infective preparations free from the proteins, although attempts to do so have been made by many different methods. There is no conclusive test for purity, but there are accepted tests for demonstrating inhomogeneity, such as behaviour in centrifugal and electrophoretic fields. Purified preparations of some viruses pass all tests, and although none alone would be sufficient to draw any conclusions, taken all together they provide a mass of evidence in favour of identifying the proteins with the viruses. There is, in fact, no evidence at all against this view, although, as we shall see later, the exact relationship between the virus particles in purified preparations and those as produced in the infected plant is a matter of some uncertainty. With some viruses, there is little doubt that purification leads to the linear aggregation of small particles to produce rods of various lengths, while with others purification seems to lead to the production of non-infective particles. Thus, while it would now be unreasonable to regard the proteins as distinct from the viruses it is reasonable to question the validity of attributing to the viruses in the plant all the properties characteristic of purified preparations.

Chemical Properties

Table 3 gives the mean values of elementary analyses made on the seven different viruses which have been sufficientlty purified for such figures to have any significance. The figures for carbon, hydrogen and nitrogen are similar to those generally found for proteins, and significant differences exist only in the figures for phosphorous and carbohydrate. After disruption with alkali or acetic acid, material with the general properties of nucleic acid can be isolated from preparations of each virus in sufficient amounts to account for all the phosphorus and carbohydrate. It seems that the viruses contain only two essential

TABLE 3

Elementary Analyses of Purified Virus Preparations

Virus	*Carbon*	*Hydrogen*	*Nitrogen*	*Phosphorus*	*Carbohydrate*
Tobacco mosaic	50%	7.3%	16.5%	0.5 %	2.5%
Potato X	49%	7.4%	16.4%	0.45%	2.7%
Potato Y	50%	—	16.0%	0.4 %	3.0%
Bushy stunt	49%	7.7%	16.1%	1.4 %	5.5%
Tobacco necrosis	45%	6.5%	16.3%	1.65%	6.5%
Tobacco ringspot	51%	7.6%	14.6%	4.1 %	18.0%

constituents, nucleic acid and protein, and this chemical simplicity is one of the features that separates them most sharply from even the simplest organisms. The nucleic acid seems to be of the same general type in all the viruses studied, though detailed work has been done only on tobacco mosaic virus. It is related to yeast nucleic acid rather than to thymus nucleic acid, which is characteristic of nuclei, for it contains a pentose and not a desoxy-pentose. There is evidence that the nucleic acid is not identical with that obtained from yeast, though further work on the precise identification of the carbohydrate, and the bases will be needed before this is established.

The ease with which the nucleic acid can be separated from the protein part varies with different viruses. With tobacco ringspot virus of which over 40 per cent. seems to be nucleic acid, exposure to strong salt solutions is all that is necessary. With the others the bond between the two components is stronger, but again, differs with different viruses. Many treatments that separate the two components of tobacco mosaic virus and potato virus X, for example, fail to do so with tomato bushy stunt or tobacco necrosis viruses.

Work on the amino-acid composition has been done only with tobacco mosaic virus. When this virus is denatured by heat, a series of protein fractions can be obtained which precipitate in different conditions. These are readily hydrolysed by proteolytic enzymes that have no effect on the intact virus ; similarly, the free nucleic acid is hydrolysed by nuclease, which does not break down the intact virus. The ordinary strain of tobacco mosaic virus has been found to contain 2.4 per cent. alanine, 9 per cent. arginine, 2.6 per cent. aspartic acid, 6.7 per cent. cystine or cysteine, 5.3 per cent. glutamic acid, 6.1 per cent. leucine, 6 per cent. phenylalanine, 4.6 per cent. proline, 6.4 per cent. serine, 5.3 per cent. threonine, 4.5 per cent. tryptophane, 3.9 per cent. tyrosine and 3.9 per cent. valine ; the following amino-acids are believed to be absent : glycine, histidine, hydroxyglutamic acid, hydroxyproline, lysine and methionine. Strains closely related to the ordinary strain, such as tomato aucuba mosaic virus, appear to have similar amino-acid compositions, but significant differences have been found between the compositions of remotely related strains. A strain that attacks plantain, for example, contains 2 per cent. methionine and 0.55 per cent. histidine, both of which are absent from ordinary tobacco mosaic virus, and contains 4.3, 3.5 and 6.4 per cent. of phenylalanine, tyrosine and tryptophane respectively. Similarly, cucumber viruses 3 and 4, which are also remotely related to tobacco mosaic virus, contain these three amino-acids in amounts different from either tobacco mosaic virus or the plantain virus.

Physical Properties

Purified preparations of tobacco mosaic virus have many unusual properties, most of which indicate that the particles present are greatly elongated. They have anomalous viscosity and diffusion, and they are thixotropic and show striking optical phenomena. When viewed in ordinary light, solutions show an intense satin-like sheen, especially when shaken, while in polarised light they are either spontaneously birefringent or show the phenomenon of anisotropy of flow (flow birefringence). When concentrated solutions are allowed to stand undisturbed, they separate into two liquid layers (Fig. 15). The upper is the more opalescent, though it is more dilute than the lower. This indicates a greater optical homogeneity of the lower layer, suggesting a regular arrangement of particles. This regularity is more strikingly evident when the solutions are observed in polarised light, for the lower layer is liquid crystalline while the upper layer is not birefringent when stationary, but becomes so if gently agitated, when the rod-like particles become orientated along lines of flow.

The separation of layers from an originally homogeneous fluid occurs only when the concentration is so great that the particles are unable to move freely in all directions. The first stage shows as the production of small birefringent droplets or tactoids. Each of these is a single liquid crystal in which the particles are arranged parallel to one another. The concentration of virus in these tactoids is slightly higher than in the surrounding fluid, so that their specific gravity is slightly higher and they fall to the bottom of the tube. This process continues until the concentration is reduced to a level at which the particles can rotate freely in all directions. Brownian movement will then keep them distributed at random, so that the upper layer is not birefringent unless some force is applied to orientate the rods. In the bottom layer this orientation is spontaneous, for the concentration is such that the particles are unable to move freely, and to accommodate themselves in the available space they are forced to pack parallel to one another.

We have already seen that true crystals, which almost certainly consist largely of virus, are common in the cells of infected plants (Fig. 16). In sharp contrast to this, no true crystals of the purified virus have been produced *in vitro*. When solutions are concentrated there is a smooth gradation from a mobile birefringent fluid to a stiff gel, but there is no separation of a solid phase in equilibrium with the solution. The virus can be precipitated in solid forms by the addition of neutral salts and by agents as diverse as acids, clupein, salicylate, ribonuclease, nicotine, arginine and heparin. These precipitates are all fibrous and birefringent. Those produced by acid and salts were originally described as crystals, but they lack the full three-dimensional regularity of true crystals. The arrangement of virus particles in these fibres is essentially similar to that in the liquid crystals, particles lying parallel to, and equi-distant from, one another, but with no regularity of arrangement in the direction of the length of the particles. As usually produced by precipitation with acid or salts, the fibres are fairly regular, needle-like structures, pointed at each end, and averaging about 40μ long and 0.4μ wide. They do not seem to be produced by the usual process of crystal growth but by the more or less regular disruption of a gel. Attempts to increase their size by slow precipitation methods have failed; indeed, if neutral solutions are kept undisturbed while the salt content or acidity is gradually increased, there is no precipitation of a solid phase. Instead, the whole preparation passes into a fairly rigid gel, which changes instantly into a suspension of needles when stirred. With substances such as nicotine or clupein, which combine with the virus to produce insoluble complexes, the precipitates are often more obviously fibrous. If left undisturbed, flexible fibres some centimetres long are formed, but these can be disaggregated to the more typical needles by shaking.

In these respects all the strains of tobacco mosaic virus, as well as the remotely related cucumber viruses 3 and 4, behave similarly. Potato viruses X and Y, hyoscyamus virus 3 and severe etch virus, also form liquid crystals and show anisotropy of flow, though these have all given amorphous, instead of fibrous, solids when precipitated with acid or salts. It is perhaps worth noting that all the purified viruses with greatly elongated particles have elementary analyses similar to tobacco mosaic virus, that is, the ratio of nucleic acid to protein is probably similar in all. This may be only fortuitous, but the viruses so far studied which contain a larger proportion of nucleic acid behave differently.

The first of these to be isolated was tomato bushy stunt virus, and it gave the first unequivocal crystals. Purified preparations have no anomalous physical properties and show no phenomena characteristic of elongated particles. Crystals are easily produced by making use of an unusual property, the greater solubility of amorphous precipitates at 0° C. than at 20° C. The precipitate that separates when ammonium sulphate is added to a solution of tomato bushy stunt virus at room temperature is amorphous. If the fluid is then cooled to 0° C., the precipitated material dissolves, but if kept at 0° C. for some time the virus crystallises in the form of rhombic dodecahedra (Fig. 16). If the concentration of salt is such that crystallisation is slow, crystals up to 1 mm. across are readily made. This virus also forms insoluble complexes with various materials; the complex with clupein crystallises as rhombic dodecahedra, with heparin as isotropic prisms, while the complex with ribonuclease has not been crystallised.

Work on plants suffering from tobacco necrosis has produced a wide range of different crystalline products. This disease is unusual in many respects. It can be caused by a number of distinct viruses, which are serologically unrelated and have different properties, though they give similar figures for elementary analyses, and each of which seems to occur in a number of strains. No hosts are known in which these viruses give a true systemic infection. In naturally infected tobacco plants, the viruses are restricted to the roots or to leaves in contact with the soil. The upper leaves of tobacco, as well as of many other plants, are susceptible if inoculated with the viruses, though the only symptoms produced are necrotic local lesions (Fig. 17). Of a number of cultures of tobacco necrosis viruses that have been purified, all except one have been crystallised by the same method as that described for tomato bushy stunt virus. The different cultures give characteristic birefringent crystal forms, which include thin lozenge-shaped plates hexagonal prisms, dodecahedra, bipyramids (Fig. 18), and thin round laminæ. The exception, which has never crystallised when precipitated with salts, readily crystallises under other conditions. When sedimented in the ultra-centrifuge, for example, this virus

differs from the others in producing a crystalline pellet with the characteristic appearance shown in Fig. 19. Also, if salt-free solutions more concentrated than one per cent. are stored in the cold, they begin to deposit crystals after a few weeks. Crystal growth will continue in these conditions for some months to produce individual crystals up to 6 mm. in length (Fig. 20).

Another virus with spherical particles which seems to behave similarly to some of the tobacco necrosis viruses, is southern bean mosaic virus, which has been crystallised in the alternative forms of rhombic prisms and bipyramids. Purified preparations of tobacco ringspot virus, which also seems to have spherical particles, have not crystallised. This may simply reflect the instability of the virus *in vitro* rather than any inability to form crystals, for characteristic crystalline inclusions are found in plants suffering from ringspot. This virus is more easily denatured than the others we have been discussing, so that comparisons are difficult to make.

The Sizes of Virus Particles

In many accounts of viruses there are to be found tables or diagrams in which the sizes of different virus particles are recorded with great precision. These are largely fallacious, because they suggest that our knowledge of this subject is much more definite than it actually is. This fact will be obvious to the discerning reader, who will note that the size attributed to some viruses, particularly tobacco mosaic, has varied within wide limits in successive tables published by the same writers. The truth is that nothing is known about the size of the particles of most plant viruses except that they are too small to be resolved by microscopes using ordinary light, and that the size of no virus particle is known with certainty. Of the few that have been studied in any detail, we can say that the size of some is known within fairly narrow limits, while that of others still remains a matter of speculation and controversy. Broadly speaking, the first group contains those with spherical particles such as tomato bushy stunt and the tobacco necrosis viruses, while the second contains those whose purified preparations contain rod-like particles, such as tobacco mosaic virus and potato virus X.

Most work has been done with tobacco mosaic virus, and the sizes suggested for its particles are about as numerous and varied as the workers engaged on the problem and the methods they have used. The first attempts to estimate size were made by filtration methods, by determining the smallest pores in graded collodion membranes through which the virus would pass. Later, this was reinforced by measurements of the rate of sedimentation in the ultra-centrifuge. The filtration end-points and the sedimentation constants were found to vary with different preparations of the virus, and the particle sizes calculated from the two types of measurement differed greatly. These calculations were all made on the assumption that the virus particles were spherical, and that the solutions possessed normal physical properties. The discovery that the particles were elongated and that solutions were anomalous in all their properties, invalidated all the previous estimates. Since then attempts to estimate size have been made in many different ways, and there has been a number of confident statements about the " molecular " weight of the virus, but the net result has been to gain a reasonably accurate measurement of the width of the particles and to show that their length is variable within wide limits. Presumably there is a lower limit to the size of the particles ; in other words, there is presumably an equivalent to a virus molecule but we have little idea what it is, and there is no doubt that most measurements have, in fact, been made on molecular aggregates.

The most precise measurement of width has been made by X-ray diffraction methods which set a maximum of 15.2$m\mu$ for the dry particle. Electron micrographs also indicate a width of this order, but the resolution is not good enough for accurate measurements ; they also show that the particles vary in length (Fig. 21), but the exact significance of length measurements made by this method is uncertain. Solutions must be dried in the form of thin films before micrographs can be made, so that there is ample opportunity while preparations are being made for changes in length to occur. Measurements of sedimentation and diffusion constants, of viscosity, of optical properties and filterability, have given reasonably constant results on preparations made in any one way, but results vary widely with different preparations, suggesting that the average length of the particles depends on the methods used for making that particular preparation. This is confirmed by electron micrographs : preparations made by the usual methods and which show the phenomenon of anisotropy of flow readily, give micrographs in which the majority of particles are 280$m\mu$ long or longer. It is,

however, highly probable that these, as well as the longer particles that are produced by more drastic treatments, are aggregates. By taking suitable precautions, preparations of the virus can be made that show little or no anisotropy of flow. These give smaller sedimentation constants than those previously found for the virus, and their electron micrographs show the presence of few particles as long as 280$m\mu$. Many, indeed, are but little longer than they are wide. These preparations are readily changed into ones showing strong anisotropy of flow, and this change is accompanied by a corresponding increase in the length of particles shown in electron micrographs.

We have already seen that true crystals are common in plants suffering from mosaic, but that only liquid crystals have been produced with purified preparations of the virus. This also suggests that there is a change in the physical state during the process of isolation. It seems probable that, as produced in the plant, the virus particles may not be significantly rod-like, but when exposed to conditions in expressed sap and the processes of purification, these small particles aggregate linearly to produce the elongated particles responsible for the characteristic properties of the isolated virus. The precise nature of the change leading to this aggregation is still uncertain, but the most likely explanation is that in the plant the particles are chemically more complex than the nucleoprotein of the purified preparations. In the plant, the nucleoprotein is probably combined with some other substance or substances, presumably inessential for infectivity, whose removal sets free groups in the virus particles which can then combine one with another. Thus, aggregation to form elongated particles may be an inescapable result of purification, and the length of the particles may be a direct measure of the chemical purity of a preparation. Only further work can determine this, but at present, the most that can be said about the size of tobacco mosaic virus particles is that, when dry, they are approximately 15$m\mu$ in width and vary in length from an unknown minimum to over 1,000$m\mu$.

Much less work has been done with the other viruses whose purified preparations are liquid crystalline, but it is probable that they also vary in length in much the same way as tobacco mosaic virus. It is certain that the particles of potato virus X, for example, increase greatly in length during the processes of purification, but again, we have no knowledge as to the size of the original particles as they are formed in infected plants.

Much more confident statements can be made about the size of tomato bushy stunt virus, for the physical properties of different preparations are constant and calculations from measurements of different properties all suggest particles of about the same size. Most of these measurements, however, relate to the size of the particle when dry: they indicate a spherical particle of approximately 26$m\mu$ in diameter and a weight equivalent to a molecular weight of about 7,500,000. It seems likely that in solution the effective size of the particles is larger than this, for they seem to be hydrated, each gram of dried virus probably being associated with approximately 0.76 grams of water.

Other viruses which seem to have spherical particles are probably smaller than tomato bushy stunt virus. Tobacco ringspot virus with a specific gravity of 1.57 has a sedimentation constant of 115 Svedberg units, corresponding to a particle of diameter 19$m\mu$ and weight equivalent to a molecular weight of 3,500,000. Some of the viruses that cause tobacco necrosis have a specific gravity of 1.35 and a sedimentation constant of 112 Svedberg units, corresponding with particles of diameter 24$m\mu$ and a weight equivalent to a molecular weight of 5,800,000. The tobacco necrosis virus that produces large crystals from distilled water seems to have the smallest particles of any plant virus yet studied. It has a sedimentation constant of only 49 Svedberg units, corresponding to a particle of 16$m\mu$ in diameter and a weight equivalent to a molecular weight of only 1,800,000. X-ray diffraction diagrams made on single crystals indicate a particle slightly smaller than this. These measurements were all made on purified preparations that had lost most of their infectivity, so that their bearing on the size of infective particles is uncertain. However, it is likely that this type of inactivation, in which serological activity is unaffected, results from internal changes in the virus particles rather than from any gross alterations in structure and size. Such changes can be produced in all the viruses that have been studied by treatment with such agents as formaldehyde and nitrous acid, or by irradiation with X-rays or ultra-violet light; with bushy stunt and tobacco necrosis viruses, however, they are also readily produced by such treatments as heating and ageing, which have no similar effect on the anisotropic viruses tobacco mosaic and potato X. With

these two, the loss of infectivity produced by these treatments is closely correlated with disruption of the virus particles and loss of all characteristic properties.

The Multiplication of Viruses

Knowledge on the physiological activities of viruses in their hosts now lags considerably behind that on their physical and chemical properties *in vitro*. We know something of the factors that influence the rate and extent of multiplication, but there is little experimental evidence with a direct bearing on the mechanism of reproduction. Any discussion of this subject, therefore, must be largely speculation.

The viruses that have so far been isolated differ so strikingly from even the simplest organisms that it is unlikely that they reproduce in the same manner, *i.e.*, by individuals increasing in size and dividing into two as in the binary fission of cells. In many ways the virus particles resemble constituents of organisms more closely than they resemble the organisms themselves. Chemically they seem to be single substances, nucleoproteins, in sharp contrast to the wide range of different materials contained in the smallest bacteria. Structurally also the particles resemble molecules rather than organisms. X-ray diffraction diagrams show that the particles of tobacco mosaic virus are solid structures in which the constituent units are arranged with a perfect three-dimensional regularity. This fixed internal structure is similar to that found in large molecules, such as those making up animal or plant fibres, and contrasts vividly with the variable internal structure of organisms. Such facts all make it probable that the multiplication of viruses is a process more akin to that whereby the individual constituents of normal cells are produced than to the actual multiplication of whole cells. Binary fission, however, can only be regarded as the last stage in a process whereby one cell becomes two. Both before and after fission, there is an increase in the quantities of many components of cells. Indeed, apart altogether from cell division, there is in living cells continual change leading to the production of constituent substances, including proteins. Until we know more of the processes whereby these are synthesised, it is unlikely that we shall be able to form any accurate picture of virus multiplication.

A theory that has gained some support is that viruses are merely autocatalysts, which multiply by changing inactive precursors into viruses. The analogy used for this is the production of some proteolytic enzymes. Trypsin, for example, is not produced in the pancreas as such but as a proteolytically inactive substance, trypsinogen, which is converted into trypsin by the active enzyme. Thus, if a little trypsin is added to a lot of trypsinogen, the whole changes into trypsin. There are, however, powerful arguments against applying this to viruses. The inactive precursors resemble the enzymes themselves in many ways and often change into them apparently without having the enzymes introduced from outside. By contrast, no substances so closely resembling the viruses have been found in healthy plants of susceptible species. Again, on this autocatalyst theory, we would have to assume that all the plants that are susceptible to any given virus normally contain the postulated virus precursor; also individual plants would need to contain precursors for all the viruses to which they are susceptible. Indeed, we would need to go further and postulate a precursor for every virus strain, for with proteolytic enzymes it is known that the precise enzyme produced is determined solely by the precursor and not by the enzyme used to activate it. For instance, there are various trypsin-type enzymes, each of which has its own specific precursor. If trypsin is added to chymotrypsinogen, this changes to chymotrypsin and not to trypsin; similarly, if chymotrypsin is added to trypsinogen, this changes to trypsin and not chymotrypsin. If one enzyme is added to a mixture of precursors, then the final result is a mixture of enzymes in the proportion of the respective precursors. This is very different from the results obtained by infecting plants with mixtures of virus strains, for these depend on the particular virus strains present in the inoculum and not on the host plant. If plants contained specific precursors for each strain one would expect a different result; infection would merely transform the specific precursors of strains of, say, tobacco mosaic virus into the individual strains, so that regardless of the inoculum the end result would be the same mixture of virus strains. It is true that the changes we now regard as akin to mutation could be explained on the basis of activating precursors, but on this view it seems impossible to account for the fact that bulk cultures of different strains remain relatively constant and recognisably different over periods of years.

We have seen that the individual virus

particles have a regular internal structure corresponding to that of a crystal. Now crystal growth is a well-known phenomenon and the addition of crystal " seeds " into solutions is a standard method of producing large numbers of similar crystals. Thus, we might regard a virus particle as behaving like a crystal focus, which finds within the infected cells the necessary building materials, causes these to be orientated in a suitable manner and to " crystallise " out in the pattern of the original particle. This may give a plausible and convenient picture for the final stage in the production of virus particles, but it is almost certainly an over-simplification. Before this stage, which can be regarded as analogous to the final stage of fission in the multiplication of cells, there are probably considerable modifications of the metabolic activities of the infected cell. In normal cells, protein synthesis proceeds along specific lines, each type of cell producing certain characteristic proteins. This production of characteristic proteins is thought to be attributable to the specificity of the intracellular proteinases, the resulting proteins being those stable in the presence of these enzymes. It seems likely that the introduction of a virus particle might alter the direction of synthesis, so that new products are formed, some of which ultimately enter into the composition of the virus particles themselves.

It may be that our present conception of viruses as self-reproducing nucleoproteins is yet another over-simplification. The total functioning entity may be the infected cell and not the individual virus particles which *in vitro* correspond to molecules or molecular aggregates and which seem devoid of any metabolic processes. These may be only the chemical minimum that can initiate the chain of reactions in susceptible cells which finally leads to the production of more virus, and to the other effects that we recognise as diseased conditions. During the course of purification many substances are discarded as impurities ; most of these may be normal plant constituents, but, for all we know, some are specific products of infected cells. *In vitro* viruses can combine reversibly with many substances, including proteinases and other enzymes, and this they may also do within infected cells. Indeed, we know that virus does occur in combination with other substances. Recent work has shown that, after extracting the sap, the fibrous residues of infected plants contain more virus than is obtained from the sap itself, though special treatments are needed to bring it into solution. Also, the ready aggregation of tobacco mosaic virus is most simply explained by postulating the removal of some other substances from the virus nucleoprotein. It seems likely that on entering a susceptible cell a virus particle combines specifically with some substance or substances, and that such combination is an essential step towards multiplication. If we assume that unrelated viruses combine with different substances, whereas related strains of one virus combine with the same ones, then we have a ready explanation for the fact that plants infected with one strain of a virus are resistant to infection with a second, though they are still susceptible to unrelated viruses. Much more work will be needed on the behaviour of viruses within the plants, however, before any of the suggestions made in this section can be refuted or confirmed.

OBITUARY

Thomas Allen Woolterton Reed, senior examiner in Shorthand for the Royal Society of Arts, died on December 30th, 1945, at the age of 85 years. He had been a Shorthand enthusiast all his life, and for 59 years had been connected with the Royal Society of Arts examinations. Shorthand, to Allen Reed, meant Pitman's Shorthand, but he was a man who did not do things by halves and so made himself familiar with other systems, past and present. Shorthand was both vocation and hobby, and his introduction to this form of writing through his father, Thomas Allen Reed, was in the days when Shorthand was a social rather than a commercial asset. Reed kept abreast of the times and fully appreciated that, to-day, the test of good Shorthand is the transcript of the Shorthand notes. For vocational purposes, apart from his work as examiner, Allen Reed used his Shorthand as a reporter and was employed on various Government commissions, going five times to India—including the Delhi Durbar—and once to South Africa on the Hospitals Commission during the South African War. He was a sportsman and a practical exponent of the ancient sport of falconry—a sport which occupied his spare moments for 70 years of his life—and, early in the century, hunting with a goshawk he had as much sport, over a shoot that he rented, as would be obtained by the most expert of guns. For the last 20 years, he

has been immersed in village life, yet strenuously occupying himself on the Society's business. Allen Reed died in harness, marking Shorthand scripts up to December 29th, 1945. Though it will be hard to find his equal, his rest is well-earned.

R. W. H.

DR. J. M. VILLASANTE.—The Society's examinations have recently suffered another loss by the sudden death at West Horsley of Dr. Julian Martinez-Villasante y Navarro. He had conducted for many years both the oral and written examinations of the Society, and always took the keenest personal interest in this work. He will be greatly missed by his old friends on the staff. He was born in Madrid in 1876 and educated at the Universities of Madrid and Santiago. He was lecturer in the Spanish language and literature at Cambridge University from 1907 to 1917 and Senior Lecturer in the Department of Spanish studies at King's College, University of London, from 1913 until he retired in 1936.

H. T. B.

GENERAL NOTE

LEVERHULME RESEARCH FELLOWSHIPS, 1946.—Application is invited for Fellowships and Grants in aid of research. The Fellowships and Grants are intended for senior workers who are prevented by routine duties or pressure of other work from carrying out research. They are limited to British-born subjects normally resident in Great Britain. In exceptional circumstances the Trustees may waive the condition as to residence.

The Trustees are also prepared to consider applications from groups of workers engaged upon co-operative programmes of research particularly from those engaged upon long-distance programmes or in institutions in which the normal facilities for research have been curtailed by the war. The duration of the awards will not normally extend over more than two years or less than three months and the amount will depend on the nature of the research and the circumstances of the applicant.

Forms of application may be obtained from the Secretary, Dr. L. Haden Guest, M.C., M.P., Leverhulme Research Fellowships, 7, Bedford Row, London, W.C.1. Applications must be received on or before March 1st, 1946. Awards will be announced in July and will date from September 1st, 1946.

CORRESPONDENCE

THE PROBLEM OF PICASSO.

I have read with interest Mr. Herbert Read's Apologia for Picasso in the January number of the *Journal*, and approve of his application to Picasso of Jung's phrase as to "shattering nightmares."

Having for over a quarter of a century represented South Kensington in Parliament, I have always taken the greatest interest and pride in our world-renowned South Kensington Museum and its special exhibitions. I accordingly went to see for myself shortly before the closing of the Exhibition the Picasso and Matisse pictures, as I was anxious if possible to ascertain why these pictures were there, and, to quote Mr. Justice Asquith in a recent letter to the *Times*, whether they had any claim to be "significant" and if so, significant of what. An answer to my first question was immediately available from a poster at the entrance, as well as from the catalogue, where it was stated that the exhibition was "Under the Auspices of the British Council," which, it will be remembered, is a body subsidised by the British Government to the tune of about £3,000,000 a year. In answer to the second question, I would suggest that the pictures are perhaps "significant" of the post-prandial resultants of Christmas and other festivities. Even in these strictly rationed days, it cannot have been an altogether exceptional experience after retiring to rest on the night succeeding a festival, for a series of remarkable pictures and images often to pass before one's semi-conscious mind. First in our gallery of imagination we may see a siren beckon us and then, as we approach nearer, we find ourselves in a dissecting room, with noses, legs, breasts, torso and feet all jumbled up, with radiators, fire-irons, window frames, armchairs and other junk, trimmed inconsequently with ladies' hats; and through it all, at all sorts of angles and places, an alarming series of piercing eyes. Some such phantasmagoria may well be the result of over-indulgence, and the "significance" of these pictures may perhaps show the cleverness of the artists in depicting our "shattering nightmares" on canvas as a warning against intemperance and an urge for moderation. But——

Why under the auspices of the British Council?

Why in the National Galleries of South Kensington?

BROUGHSHANE.

As a student of Dr. Herbert Read's own vocabulary in art criticism [*Education through Art* and *Art and Society*] may I suggest that terms borrowed from a clinical form of psychology are no more appropriate to æsthetic criticism than are the list of words he quotes from *The Times* in " The Problem of Picasso " ?

The real problem is more comprehensive : and involves an element in art criticism, i.e., " fitness for purpose." Are " purge paintings " (1) suitable for an exhibition ? (2) sponsored by a government official ? (3) in a public gallery ? (4) with free admission to children ? With these questions more or less in mind some of the epithets in the letters to the press are not inapt. As a critic of graphic arts Dr. Read shows a tendency to stray through the looking glass e.g., he sees " symmetry " in these paintings of Picasso. In reality it is the negation of symmetry (in the sense of *balance*) that is the cause of such a just epithet as " tormented."

It is not surprising that an art critic who can classify Blake as *introvert* should quote his Tiger when claiming that the disintegrated figures of Picasso's present phase are examples of symmetry.

IRENE MAGUINNESS.

We should be grateful to Mr. Read, writing in your issue of January 18th, for having explained so clearly the genesis of these latest productions of Picasso. He says, referring to the æsthetically lethargic English, " starved stomachs do not take kindly to rich food " the inference being that Picasso's revelations are the rich food after digestion—a nasty notion however just, and one we do not feel strong enough to enlarge upon.

It is not easy for an ordinary intelligence to grasp fully the abstruse implications of such mental exercises as going " deep beneath the surface of conscious perception to explore the terrain of the collective unconscious," but now that we know, on Mr. Read's authority that Picasso performed this ghostly adventure and that it was from " the unassuaged chaos " found there that he " snatched his disturbing images " we begin to feel our feet, so to speak ; and when, further, we find that in this adventure of exploration and the subsequent pictorial recording of the treasures found, the artist was in a state of trance—well, the whole business becomes clear.

Picasso, in a state of trance, delved into these hypothetical regions and there his brain became impregnated by imaginary horrors ; the embryo grew, until the artist feeling an uncontrollable urge for relief from his burden, delivered himself of it and exhibited the result to the world, where it was pronounced by some, an abortion, by others a new species. That seems to be all there is in this pother.

Mr. Read seems to think that because thousands flocked to see this mess of images culled from unassuaged chaos, it was approved, but he ignores that which his intimate knowledge of psychology should have told him, that the populace always has found a fascination in horrors and monstrosities, not from love but from natural or morbid curiosity ; and helped by the useful publicity given to the show, the numbers grew. If an entrance fee had been charged the profits in hard cash would have been most satisfactory.

There is an ingenious little apparatus called by the infelicitous name of Designograph, a lineal successor of the delight of our childhood, the Kaleidoscope, in which odd and pleasantly coloured heterogeneous scraps when viewed through the eye-piece resolved themselves into interesting and often charming symmetrical patterns by a system of reflections in little mirrors built into the apparatus. If any of these mirrors became displaced or broken the result was a meaningless jumble of distorted reflections of the scraps, retaining only their quality of pleasant colour. Now, perhaps Picasso's reflecting brain—but, no. Mr. Read has enlightened us.

FRED H. ANDREWS.

NOTES ON BOOKS

WITCHCRAFT IN ENGLAND. By Christina Hole. Batsford. 1945. 21s.

This is a rather terrible book. Miss Christina Hole is an authority on folklore and customs, and here, in *Witchcraft in England*, she has set down an exhaustive and detailed study of all the beliefs in witches and witchcraft that have ever obtained in this country, together with all its dark records of witch-finding, witch-baiting and witch-murdering. The effect is one of such cumulative horror that the book in the end repels rather than attracts, and even the fascination

of the *macabre* (a stimulus best taken in small doses) ceases to ensnare. One feels that the subject is too evil and (to use a now forgotten vogue-word) too shame-making for such continuous contemplation ; that the student may dip with interest into the tales of the Lancashire witches, the Somersetshire witches, or the Wiltshire wizards, setting each group against the background of its county folk-lore, but that to concentrate upon the witch records, not of one or two counties but of the country itself, is to tell too long and too ugly a tale.

If, however, the thing was worth doing, it could not have been done better. Miss Hole shows how widespread was the witch belief and how strong a hold it once exercised over all sections of the community. Its basis was a passionate faith—the witch's faith in her power to do evil and the victim's equally firm belief that such evil could inescapably be wrought upon himself. Its horrible rites and observances were not so much anti-Christian as pre-Christian, going back to the magical rites of fertility cults practised in pre-historic times ; and in this country, it is worth remembering, those rites were never so unholy and Satanic as on the continent. One interesting characteristic of the English witch was the usage of domestic familiars, the cat and dog, which is peculiar to England and especially to the eastern counties—a queer perversion of our English love of animals and fondness for keeping pets. Miss Hole deals with the familiar at some length, and also with the loathsome trade of the witch-finder, who pricked for the devil's mark upon the bodies of these crazed and wretched souls. Newcastle-on-Tyne, for example, paid its professional pricker 20*s*. for every witch unmasked, and he had brought on his own confession at least 220 women to death before he at last, in his turn, was hanged. Another interesting point she makes is a vindication of King James I against the popular conception that he was the most cruel and bigoted of witch-hunters : he was on the contrary, in spite of his *Dæmonologie* and the severe Witchcraft Act of the second year of his reign, less credulous than the majority of his subjects in this matter, and his interventions in witch-trials were nearly always on the side of common sense and justice. Miss Hole also gives a full account of the extraordinary career of the sixteenth-century astrologer, Dr. John Dee, " a man of deep learning and a student of the secret arts," who was favoured with the protection of Queen Elizabeth. He chose the date of her coronation for her and was summoned to Windsor to reassure her on the harmless nature of Halley's comet, when it appeared in 1577 and was feared to bode ill for her reign. He was also the prototype of that engaging rascal, Subtle, in Ben Jonson's *Alchemist*.

The whole grim story is carried through to the time of the final decline of the popular belief in witch-power. In 1684 the last execution for sorcery was carried out in England, at Exeter, on a wretched woman named Alice Molland ; and in 1736 King James's Act was repealed and witchcraft ceased in this realm to be a statutory offence. Henceforth, as Miss Hole clearly points out, such prosecutions as those which occasionally take place to-day are for pretence to magical powers only and not for their actual exercise. It is pathetic to learn, with regard to this Act of Repeal, that kind and wise John Wesley denounced it on the ground that giving up witchcraft was giving up the Bible.

This exhaustive study is illustrated by a series of fantastically imaginative drawings in monochrome and line by Mervyn Peake. This is a new departure in book illustration and one wonders if it has been entirely successful. Obviously the subject could not lend itself to those delightful reproductions of the modern photograph and the old line-engraving which are the hall-mark of a Batsford book. But although the drawings have undoubted power and originality, they once again repeat too often the *macabre* note of the book, and one wearies of study after study of evil and imbecile and cretinous old women.

There are alas ! certain horrors with which it is not wise to sup too full.

NORAH RICHARDSON.

EROSION IN THE PUNJAB ; THE CAUSES AND CURE. Civil and Military Gazette, Ltd. Lahore. 1944.

In the Eighties and Nineties of last century, some at least of those who had any acquaintance with the Punjab would have heard of the Hoshiarpur Chos and the fantastic nature of the Erosion which had eaten cliffs of bizarre shape into the hillsides. Very large areas of agricultural land went out of commission, since the Government was unwilling to interfere with the actions of the population which resulted in a gradually increasing burden of overgrazing, lopping and firing in the forest areas. It is not surprising therefore to learn that Hoshiarpur is the first District in the Punjab in which Soil Conservation Works

were organised. The present position of the Province is admirably dealt with by Sir Harold Glover, late Chief Conservator of Forests, in his book " Erosion in the Punjab : the Causes and Cure." H.E. Sir Bertrand Glancy, Governor of the Punjab, in a preface, writes that the author " with his wide experience of the Punjab, is well qualified to explain and bring into relief the growing menace of soil erosion . . . for erosion is a canker that has been eating remorselessly into the vitals of the Punjab. It is scarcely possible to exaggerate the danger of permitting it to advance still further. The disease has now been diagnosed and effective remedies have been prescribed. But so far little more than the fringe of the evil has been touched. When the life of the whole Province is imperilled no individual can be allowed, through selfishness or indifference, to stand aside."

This is, at last, plain speaking from the highest quarter. It is a pity the Head of the Province did not utter the same words half a century ago. There were a few Officers, mostly Forest Officers admittedly, who had diagnosed the diseases, both here and elsewhere, fifty years ago ; but the decision ruled that any interference with the habits and customs of the people was unwarranted and was strictly enforced amongst officials. It is held by many that the first realization of what erosion is capable of was brought home to the public by the publicity given in the Press to America's " dust bowls," considered to be the biggest and latest example of this type of calamity in the world. A perusal of Glover's book and the mass of facts and statistics, supported by remarkable photographs, will show that the Punjab, the Land of the Five Rivers, offers a more remarkable and infinitely more varied illustration. The history of this matter during the present century is well summed up by Sir James Penny, Financial Commissioner, Development, Punjab, in a foreword he contributes to the book : " The protection of the soil has long been recognised as an object, if not the main object, of Forest policy, but in this Province the rapid denudation of the Siwaliks and the disastrous effect on the plains below led to the enactment of the Chos Act some 40 years ago to deal with the special conditions of the area. Progress, however, was slow until the fourth decade of the century when the subject began to receive increased attention." The failure of the District Officer of the past to recognize the portents is now obvious and the recent work has, in Sir James Penny's words, " done little more than blaze a trial and that only in some districts in which the problem must be faced."

The author opens his Introduction as follows : " Soon after the British occupation of the Punjab " (on March 26th, 1849, the Province was annexed) " the devastation of the forests by fire and reckless felling caused grave concern to Government. Attempts were made to preserve what was left and the more important forests were demarcated, but they form only about $5\frac{1}{2}$ per cent. of the area of the Punjab. Many are forests only in name, and almost all are open to grazing." In those early years between 1850 and 1857 it was the failure of the Settlement Officers, as for example Mr. Barnes' Settlement Report of Kangra, to record definitely the full rights of Government to the forest lands, which was responsible for the future trouble. Forest Rules were drawn up during this period for Kangra, the Rawal Pindi district and Hazara ; but the chief provisions against grazing, firing, lopping and illicit felling were not enforced. Glover continues : " Throughout the lower hills the pressure of the population on the forests has been so great as to result in their destruction. Conditions became intolerable and on April 1st, 1939, Government decided to entrust the restoration of the eroded lands of the Punjab to the Forest Department, and created a special Soil Conservation Circle for a period of five years." The author, as Head Forest Officer of the Province, then had charge of this for the first four critical years, and his book has been written as a result at the request of Government ; no one can have a closer acquaintance with the country and the facts and the results achieved, already sufficiently remarkable, his book well depicts.

Perhaps the chief reason for the present attitude is the full realization of the great danger to the widespread canalisation of the Punjab plains by utilising the water of the " Five Rivers," the sources of which, and those of their many tributaries are in the Himalaya. Erosion up there and in the foothills means silting up in the great canals and their distributors. The author has divided his subject into two parts—Part I of more general interest, dealing with Description of the Country, Soil, Climate and Vegetation, Causes of Erosion, Grazing, Direct and Indirect effects of Erosion, Duties of District Officers, Cure for Soil Erosion, Engineering Works and Forest Policy and

Acts. In Part II descriptions of methods of Soil Conservation peculiar to different Districts of the Punjab are given—this Part being of more especial value to the District Officer in charge of these areas.

Space will not permit a closer survey of this admirable piece of work. It may be confidently recommended to other parts of the British Empire and the World. Perhaps the most arresting fact, as it is one of the most comforting, is that restoration work to counteract erosion and its results does not necessarily mean the construction of expensive engineering works. Successful and often more certain results can often be attained by strict closing of degraded areas to grazing, firing and illicit fellings over a period of years, with oft astounding results, as some of the beautiful photographs will depict.

E. P. Stebbing.

El Greco. The Purification of the Temple. With an Introduction by Enriqueta Harris, and twenty-three illustrations. The Gallery Books, No. 2. Percy Lund Humphries & Co. 1944. 4*s*. 6*d*.

In this, the second of the series of monographs, the picture chosen for the study of Domenikos Theotopoulos, " El Greco," one of the several versions by the same artist, is that in the National Gallery, London. Two others, one in the Cook Collection and the other in the Church of S. Ginés, Madrid, are also illustrated and discussed. A fourth, in which he is said to have introduced portraits of Titian, Michelangelo and Raphael, is at Mineapolis, and is unfortunately not reproduced.

Being a Greek, born near Candia in Crete, his earliest work is said to reflect the manner of Byzantine icons, the Art with which he would be most familiar by his youthful environment. But later, proceeding to Italy he assumed the style of that country, studying in Venice as a pupil of Titian. From there he went to Rome where he does not seem to have been popular with the Art fraternity, perhaps because of his arrogant bearing. He is said to have offered to replace Michelangelo's *Last Judgment* in which were certain features disapproved by Pius V., with one equally good. He did not think Michelangelo was a good painter. He then moved on to Spain where he settled in Toledo. Here he was not a success at Court perhaps because of his personality, but was successful as a painter outside the august circle. The writer of the monograph briefly suggests the character of the man, who, in spite of his self-assurance yet so completely changed his style of painting. The inequality of his work is commented on by his contemporaries, and one, Polomino, said of him " What he did well, no one could do better ; what he did ill, no one could do worse." Was it perhaps that he was in advance of his time and was feeling his way towards impressionism to the disgust of his critics ?

The subject here dealt with had evidently a great attraction for him and the several renderings are very interesting as showing the progress of his style from the traditional Italian to that of Spain and his own pronounced individuality. Although Spanish painting has been richly nourished by that of Italy it yet has impressed upon it a definite native stamp ; and El Greco, a foreigner with Italian training, shows in the work of his Spanish period how greatly he was influenced by local atmosphere. It is interesting to compare his later manner of painting with that of Manet. In both there is fine drawing combined with powerful and rapid brushwork a certain disregard of detail yet expressing it.

Although brief, it is an extremely interesting monograph showing thorough and sympathetic study of the subject. There is one curious mistake in the last few words of the description of the S. Ginés version of the subject. The author draws attention to the figure of Christ " driving back the sinners with one hand and pointing to heaven with the other." This " other," the left, is dropped to hip level, turned outward with palm downward, suggestive of blessing and so perhaps intended to dispel any idea of ungoverned violence.

F. H. A.

Edouard Manet. Un Bar Aux Folies-Bergère. With an Introduction by Raymond Mortimer and fourteen illustrations. The Gallery Books, No. 3. Percy Lund Humphries & Co. 1944. 4*s*. 6*d*.

In this admirably balanced account of the artist and his work the writer, while justly appreciating his power as a painter is not entirely in sympathy with the class of subject sometimes chosen for its expression. It may be true that he was successful in communicating his " imaginative vision," but, as the writer says, his vision was often commonplace ; and the work chosen for this monograph,

masterly as it is in its rendering, presents the picture of a particularly dissolute aspect of French life. This is the life with its pageantry of colour, sensuality and tragi-comedy, to which Manet's nature responded. And yet, while in every detail the pervading atmosphere of moral laxity is expressed, the skill of the painter directed by the vision of the artist goes far towards condoning his choice of theme.

The writer says Manet "never, unless here" concerned "himself with any emotional subtilty." The reservation refers to the figure of the barmaid, but might be extended to the many figures in this picture rapidly sketched yet so vividly expressive of character, and to the portrait of Stéphane Mallarmé (Fig. 3) and the figures in Café-Concert (Fig. 4).

The impression conveyed by the study of the barmaid (Fig. 5) will doubtless vary with different people. She belongs to her environment; is just a product of this social system from which she has no hope of escape and about which she has no illusions as to her part in it. She hears, passive and unimpressed, the familiar overture murmured by the top-hatted roué, while there floats through her mind a dreamy vision of other things, out of reach but expressed in the wide-open questioning eyes, the sensitive mouth and tremulous chin. Whether or not Manet intended to convey such complex emotions in drawing the young woman, or whether, as the writer says, the girl's expression may be just that of weary boredom from sitting too long as a model, we do not know. We may interpret it as we will and may find in the artist's presentment something more than he consciously gave.

Manet travelled a good deal and he tells of his first attempt at painting, when, on a voyage to Rio de Janeiro he restored to the cargo of Dutch cheeses on board, their pristine ruddy hue, lost through damage by sea water, by painting them over with cochineal. During his travels he copied the works of many painters and through this training he not only developed his brush technique but was also confirmed in his belief in impressionist vision. There is much in his brushwork that resembles that of El Greco—the same freedom and strength with mastery of drawing; a probable result of his study in Spain.

The reproductions of portions of his pictures are excellent and very helpful in demonstrating the power and skill of the painter.

F. H. A.

SOME MEETINGS OF OTHER SOCIETIES DURING THE ENSUING FORTNIGHT

MONDAY, FEBRUARY 4..Farmer's Club, at the Royal Empire Society, Northumberland Avenue, W.C.1. 2.30 p.m. Robert Templeton, "**Dehydration.**"

Royal Geographical Society, Kensington Gore, S.W.7. 8 p.m. Air Chief Marshal Sir Philip Joubert and Lieut. Commander A. R. Glen, "**High Latitude Flying by Coastal Command in Support of Russian Convoys.**"

School of Slavonic and East European Studies, Malet Street, W.C.1. 6 p.m. Professor O. Vocadlo, "**Slavs and Germans in Central Europe. Lecture II—'The New Phase'.**"

TUESDAY, FEBRUARY 5..Hull Chemical and Engineering Society, at the Regal Cinema, Ferensway, **Hull.** 7.30 p.m. W. Morris, M.INST.C.E., F.S.I., "**Civil Engineering in Municipal Practice.**"

Institution of Automobile Engineers, at the Institution of Mechanical Engineers, Storey's Gate, S.W.1. 5.30 p.m. E. G. West, PH.D., B.SC., "**Aluminium and the Automobile Engineer.**"

Manchester Geographical Society, 16 St. Mary's Parsonage, **Manchester 3.** 6.30 p.m. T. L. Green, PH.A., B.SC., "**World Population Problems.**"

WEDNESDAY, FEBRUARY 6..Institute of Fuel, at the Institution of Mechanical Engineers, Storey's Gate, S.W.1. 6 p.m. E. C. Evans, "**The Utilization of Waste Heat in Metallurgical Furnaces.**"

Institution of Electrical Engineers, Savoy Place, Victoria Embankment, W.C.2. 5.30 p.m. G. L. Grisdale, PH.D., and R. B. Armstrong, B.SC., "**Tendencies in the Design of the Communication Type of Receiver.**"

Royal United Service Institution, Whitehall, S.W.1. 3 p.m. Dame Vera Laughton-Matthews, D.B.E., "**The Women's Royal Naval Service in the War.**"

School of Slavonic and East European Studies, Malet Street, W.C.1. 6 p.m. Professor W. J. Rose, "**Church and School in Polish History. Lecture III—18th century Enlightenment.**"

THURSDAY, FEBRUARY 7..Institution of Electrical Engineers, Savoy Place, Victoria Embankment, W.C.2. 5.30 p.m. W. Fennell, "**Fundamental Legislation for Electricity Supply to Consumers.**"

London School of Economics and Political Science, Houghton Street, W.C.2. 4.45 p.m. Professor T. H. Marshall, M.A., "**Sociology at the Cross-Road.**"

School of Slavonic and East European Studies, Malet Street, W.C.1. 6 p.m. M. Dobb, "**Outline of Russian Economic Development. Lecture III—The Decade of Construction in U.S.S.R.: the period of the Five-Year Plans.**"

The Chemical Society, Burlington House, Piccadilly, W.1. 5 p.m. (a) Dr. F. H. S. Curd and Dr. F. L. Rose, "**Synthetic Antimalarials**"; (b) Professor H. L. Riley. "**Amorphous Carbon**"; (c) Dr. C. W. Shoppel, "**The Reconversion of D-homoandrostane compounds to derivatives of allo pregnane.**"

FRIDAY, FEBRUARY 8..Chemical Society, in Chemistry Lecture Theatre, **Sheffield.** 5.30 p.m. E. J. Bowen, M.A., F.R.S., "**Light Absorption from a Chemical Standpoint.**"

North-East Coast Institution of Engineers and Shipbuilders at the Literary and Philosophical Society **Newcastle-on-Tyne.** 6 p.m. Dr. S. G. Hooker, B.SC., "**Some Aspects of Gas Turbine Development for Aircraft Propulsion.**"

Royal Institution, 21 Albemarle Street, W.1. 5.15 p.m. L. Hartshorn, D.SC., "**Radio-Frequency Heating.**"

TUESDAY, FEBRUARY 12..Chemical Society, in the Chemistry Lecture Theatre, The University, **Nottingham.** 4 p.m. Prof. A. R. Todd, D.SC., "**Synthesis in the Study of Nucleotides.**"

London School of Economics and Political Science, Houghton Street, W.C.2. 5 p.m. Professor D. Perkins, "**American Entry into the First World War: Interpretations.**"

Manchester Geographical Society, 16 St. Mary's Parsonage **Manchester 3.** 6.30 p.m. R. Dean, "**Bramall Hall.**"

WEDNESDAY, FEBRUARY 13..Design and Industries Association, at the London School of Hygiene, Gower Street, W.C.1. 7 p.m. Frederick Gibberd, "**Design and Pre-Fabrication.**"

Institution of Electrical Engineers, Savoy Place, Victoria Embankment, W.C.2. 5.30 p.m. L. G. Brazier, PH.D., B.SC. "**Joints, Sealing Ends and Accessories for Pressure Cable.**"

School of Slavonic and East European Studies, Malet Street, W.C.1. 6 p.m. Professor W. J. Rose, "**Church and School in Polish History. Lecture IV—The Ordeal of the 19th century.**"

THURSDAY, FEBRUARY 14..Institution of Electrical Engineers, Savoy Place, Victoria Embankment, W.C.2. 5.30 p.m. A. J. King, D.SC., M.SC.TECH., "**The Analysis of Vibration Problems.**"

School of Slavonic and East European Studies, Malet Street, W.C.1. 6 p.m. B. H. Sumner, "**Dostoyevsky.**"

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Candidates who have attained the age of 18 and are under 21 years of age can only be admitted as Associates. On reaching the age of 21, Associates may decide either to remain Associates until they reach the age of 24, or to apply for Membership. On reaching the age of 25 Associates must either apply for Membership or must resign from the Society.

Associates between the ages of 21 and 24 inclusive may become Members on admission by the Council and on payment of the full subscription or life composition fee prescribed in the bye-laws ; their names shall then be transferred from the register of Associates to the register of Members and they shall become entitled to all the privileges of Members and subject to the same conditions of Membership, without being required to be elected in accordance with the bye-laws.

The Annual Subscription of every Associate shall be One Guinea at least, payable in advance, for each year of Associateship at its commencement, such commencement to be reckoned from the quarter day next preceding the day of election.

Every Associate whose subscription is not in arrear is entitled—

To be present at, and take part in, the proceedings of all the Ordinary and Special Meetings of the Society and to introduce two visitors at such Meetings, subject to such rules as the Council may frame from time to time.

To receive the Society's *Journal.*

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An Associate is not authorised to use any such style or title as " Associate of the Royal Society of Arts " nor to use after his name any initials indicating such Associateship.

The form overleaf can be used either by applicants for Fellowship or Associates, as Bye-law 47 which lays down that candidates for admission must be proposed and recommended by not less than three Fellows of the Society, one of whom must be personally known to the applicant, applies to both categories of membership.

[P.T.O.

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